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Edgar T. Wherry and his Contributions to Pteridology[1]

W. H. WAGNER, JR.*

When he first became interested in ferns, Dr. Wherry was thirty years old. His background had been in chemistry and geology, and at the time he was an assistant curator in mineralogy at the U.S. National Museum. Some amateur botanists took him to see a patch of the walking fern, *Camptosorus rhizophyllus*, where it was growing on gneiss, and he became curious about its soil requirements. This led to his first publication on ferns "A Chemical Study of the Habitat of the Walking Fern" in 1916. After that Wherry became an expert on hydrogen-ion concentrations in the soils of eastern United States ferns, and he also broadened out into questions of their geography, ecology, and systematics. By the end of his career he had become an authority on North American pteridophytes north of Mexico.

In 1917, Wherry transferred to the Department of Agriculture, where he came under the influence of F. V. Coville, the Chief Botanist, who encouraged him in the study of plants. By 1930, Wherry was prominent enough in his new profession to be invited to join the Botany Department of the University of Pennsylvania. He accepted this opportunity, which was ideal for him because it represented a return to his alma mater and to his home city of Philadelphia. Wherry taught at the University until his retirement in 1955. He stayed active for many years longer than most botanists; he continued to take field trips well into his 80's and was still writing letters as late as his 90's. Only in the last few years before his death at 97 on 19 May 1982 did he lose touch.

Wherry was very active in the American Fern Society, and three-fourths of his pteridophyte publications were in the "American Fern Journal." He was President of the Society from 1934 to 1939, and he also took charge of preparing a cumulative 25-year index to the "Journal." When Maurice Broun wrote his "Index to the Ferns and Fern Allies of North America" (1938), Wherry supplied the habitat and range data for most of the species. After becoming discouraged by the poor quality of the manuals then available for identifying pteridophytes, he published one himself entitled "Guide to Eastern Ferns" (1937), which, together with the second edition, sold more than 6000 copies and did much to stimulate the popularity of ferns among naturalists and botanists. Later he wrote another valuable guide, this one for the southeastern United States. The royalties from his field manuals were donated to the American Fern Society.

Wherry did not become a major botanist of his time; he was not involved in any of the "big ideas" such as biosystematics, cytotaxonomy, and phylogeny that burgeoned during his lifetime. His approach to the study of plants was deficient in such

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[1]A series of papers in tribute to Edgar T. Wherry (19 Sep 1885–19 May 1982) was published in Amer. Fern J. 66:33–80. 1976. Biographical notes have been published in Fiddlehead Forum 9:32–33. 1982 and by Prof. Wagner in Bull. Torrey Bot. Club 109:545–548. 1982. An obituary for Dr. Wherry has been published in Bartonia, 49:1–5. 1983, the journal of the Philadelphia Botanical Club.

subjects as morphology, anatomy, cytology, and physiology, and he used the laboratory and the microscope very little in his research. He functioned primarily as a "field naturalist," as evidenced by his teaching and his publications. Over 40% of his fern bibliography dealt with geographical distributions, especially range extensions and reports of what he encountered on his numerous exploring trips. Among the many individuals who accompanied him on his pteridological field expeditions were Harry W. Trudell, J. E. Benedict, and myself. For over a third of a century, from high school student to university professor, I had the good fortune to go exploring from time to time with Wherry and to absorb his ideas of pteridophyte ecology.

In the "Fern Guide" he wrote as follows: "Sometimes . . . a fern student may have the 'thrill that comes once in a lifetime' by discovering a species in an area where it had not previously been found." Wherry passed his love for finding rare pteridophytes to others, and when the University of Virginia Mountain Lake Biological Station began its pteridology course in 1962, Wherry wrote to the class these inspiring words: "To the Mountain Lake Chapter, F. F. A. (Future Ferners of America) Greetings: At last a real study of the ferns of Mountain Lake is under way. . . . Many range extensions are to be expected there. Congratulations on yours!" He was so right—that first class and the subsequent ones (including the latest in 1982) made numerous range extensions of species in eight genera. The success of field pteridology courses everywhere in the United States, especially at Lake Itasca, MN, Highlands, NC, and at Flathead Lake, MT, owes a lot to Wherry's teaching about the roles of soil requirements and indicator species.

Wherry's most significant contributions to the study of fern distribution and ecology are those concerned with pH requirements, the subject which originally stimulated his interest in ferns. He helped to design simple kits for making field tests of soil acidity, and he showed, for example, that certain traditional reports of species growing on particular rock types were wrong. One author copied another that *Asplenium bradleyi* grows on limestone, and it took Wherry years to straighten this out and to convince pteridologists that this species is confined to acidic rocks. Thanks to his efforts to interest botanists in pH, it has become standard today for field workers to specify rock and soil types upon which plants grow. And if we wish to find a particular species, we first locate the proper substrate. We know now that it would be practically impossible for *Asplenium montanum* to be found growing beside *A. ruta-muraria*; their edaphic preferences are too different.

Oddly, Wherry paid little attention to the positive effects of disturbance and succession on pteridophytes, even though his viewpoint in general was broadly ecological. He did not seem to appreciate how influential upsets such as floods, fires, and grazing may be in enhancing the abundance and spread of many species, including botrychiums, certain dryopterids, and lycopods. Often, when a certain species disappeared from its habitat, Wherry would attribute it to vandalism or over-collecting when it was more probably a matter of simple succession.

When he tried, in his greenhouse, to duplicate the natural growth conditions of saxicolous ferns by faithfully assembling the appropriate rocks, he almost invariably failed. Had he only known what we now know, namely that most rock ferns can

grow merely in soil in pots, controlling the pH by simply mixing in limestone chips or sphagnum peat, he could have learned much more about the characters of rock ferns by culturing them side-by-side under uniform conditions. Practically everything he knew about the species he studied came from field observations.

Wherry's main contribution to pteridophyte taxonomy involved detecting hybrids in the wild. He was opposed to the wanton designation of trivial forms and varieties as illustrated by Fernald in "Gray's Manual" (1950), and he was effective in steering serious fern students away from this. His argument in "The Fern Guide" (1961) was that "since these mostly occur in association with typical plants—indeed often arising from the same rootstocks—they are not named." He distinguished between geographical varieties (what some botanists today call subspecies) and true species, as illustrated by his treatment of the decompound species of *Dryopteris*, such as *D. spinulosa* (= *D. carthusiana*) and *D. intermedia*, which by Fernald and his associates had been interpreted as varieties, *D. spinulosa*, typical variety, and *D. spinulosa* var. *intermedia*. He developed his concepts on the basis of studies of natural populations, long before modern experimental and biochemical techniques were available to confirm them.

Together with W. D. Gray, Wherry presented illustrations of intermediates, which he interpreted as hybrids, between long recognized species of spleenworts. Apparently, however, neither Gray nor Wherry was aware, or even suspected, that two of the most important of the species then recognized, *A.* ×*bradleyi* and *A.* ×*pinnatifidum*, were hybrids themselves (Wagner, W. H., Jr., Evolution 8:103–118. 1954). Both of these men, on the contrary, accepted the hybridity of the fertile *A.* ×*ebenoides* from Alabama. The most interesting of the hybrids first recognized by Wherry is *A.* ×*trudellii* (*A. montanum* × *pinnatifidum*, a beautiful example of hybrid vigor in a "sterile hybrid" which evidently can reproduce by unreduced spores. Wherry's work on *Asplenium* is honored in the name *A.* ×*wherryi* D. Smith, the backcross of *A.* ×*bradleyi* to *A. montanum*.

Under *Dryopteris* he distinguished and/or named a number of hybrids which since have become important in the genome analysis of the basic species of eastern American wood ferns. Some of these are common ferns widespread in forests and swamps. They include *D.* ×*slossonae* (*D. cristata* × *marginalis*), *D.* ×*triploidea* (*D. intermedia* × *carthusiana*), and *D.* ×*benedictii* (*D. clintoniana* × *carthusiana*). What he named *D.* ×*leedsii* and interpreted to be *D. goldiana* ×*marginalis* has since turned out to be *D. celsa* × *marginalis* (Wagner, W. H., Jr., Virginia Polytech. Inst. State Univ. Res. Div. Monogr. 2:147–192. 1970). His greatest difficulties with wood ferns involved the taxa resembling *D.* × *clintoniana*, the same ones that cause us trouble today. He nonetheless had a sharp eye for them and was the first person to recognize as distinct *D.* ×*australis* (*D. celsa* × *ludoviciana*), although for good reasons at the time he initially interpreted it as a southern variety of *D. clintoniana*. His contributions to our knowledge of *Dryopteris* hybrids are commemorated in the name *D* ×*neo-wherryi* Wagner, which is the true hybrid of Goldie's Wood Fern and the Marginal Wood Fern.

Scientifically, Wherry's influence on American pteridology was substantial. Many of today's pteridologists are indebted to his teachings as well as his inspiration. His

major contributions involved his investigations of the pH reactions of soils, distribution patterns, and his studies of various taxa, especially spleenworts and wood ferns. The American Fern Society is indebted to him for his help in many ways over more than three decades. For the general public, Wherry's field manuals and his many lectures and guided trips for amateurs helped engender a widespread enthusiasm for the natural history of pteridophytes.

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Stone Fort at Fort Totten: Last Habitat for Woodsia obtusa and Asplenium platyneuron in Queens County, Long Island, New York?

ANDREW M. GRELLER* and DAVID C. LOCKE**

In the course of documenting vegetation on the northeastern coast of Queens County, Long Island, New York, the senior author discovered two ferns, *Asplenium platyneuron* (L.) B.S.P. and *Woodsia obtusa* (Spreng.) Torrey, in what may well be their last remaining habitat in Queens County (Borough of Queens, City of New York). They were found in the weathered cement between large blocks of granite used to construct the walls of the "Stone Fort" at Fort Totten, a 19th Century coastal fortification on the Willets Point peninsula (40°47′30″ N, 73°46′40″ W). The Stone Fort now forms Willets Point, rising from the shore level to a height of thirty feet. It was built in 1862–66 as part of the seacoast defenses of New York City; photographs and a brief history of the Stone Fort were published by Alperstein (1977). Reconnaissances of the site were undertaken in the spring of 1973, in the late spring and early summer of 1978, and during the winter of 1981–82. Occasionally a few plants were measured, but a census was not attempted.

Soil samples were obtained adjacent to fern roots at two sites on the landward side of the granite wall, for elemental analysis. Stones, sticks, and obvious plant matter were separated, and a portion of well-mixed soil was ground in a mortar to a fine powder. A 1.00 g sample of each was dry-ashed at 450°C in a muffle furnace, and a semi-quantitative elemental analysis conducted with a Baird Atomics Emission Spectrograph. A just-saturated slurry in distilled water was made of each raw soil sample, and the pH measured with an Orion combination electrode and a Corning pH meter.

Further tests for sodium and chloride, indicators of saline spray, were made on samples taken near *Woodsia* roots, one from the seaward side of the granite wall, and one from the landward side. Soil samples, 1.00 g, were extracted with 10.0 ml of distilled, deionized water. The sodium content was determined by atomic absorption spectroscopy using a Perkin-Elmer 303, and chloride content by ion-selective electrode using an Orion electrode and a Beckman expanded scale pH meter.

Voucher specimens were deposited at the Herbarium of the Brooklyn Botanic Garden (BKL).

RESULTS

Fewer than twenty-five individuals of *A. platyneuron* were observed during the most recent visit (30 March 1982). These were concentrated around the central stairway connecting the three levels of the fort, between the main and upper levels, in a sheltered, moderately well lighted location. A few individuals were scattered over the rest of the main level. The plants grew from partially decomposed cement

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in joints between granite blocks. They were well rooted in the joints, to perhaps 10 cm deep. Fronds seldom exceeded 10 cm in length.

The population of *W. obtusa* numbered several hundred individuals. Plants occurred in the horizontal joints of the seaward granite wall of the fort, where sea spray and salt-laden air are features of the environment. More commonly, individuals occurred in both vertical and horizontal joints in the complex of granite walls on the main, landward side. Plants of *Woodsia* appeared to be less deeply and securely rooted than those of *Asplenium*. Commonly, young sporophytes were seen attached to gametophytes. *Woodsia* plants in winter bear a rosette of sterile fronds approximately 3–4 cm long. Fertile fronds are produced during the growing season; these regularly reach 30 cm or longer.

The substrate of both ferns consisted of a mixture of black humus and light gray fragments of cement and sands. The soil evidently arises from the mortar decomposed through weathering and from organic materials deposited by the ferns and other organisms which have gained a foothold (Segal, 1969). This is supported by our chemical analyses. The results of the dry-ashing test show that organic materials account for nearly 40% by weight of the soil sample. In addition, the emission spectrographic elemental analyses of the inorganic portions of the wall soil samples reveal silicon, calcium, and aluminum to be the major constituents and an overall composition quite similar to that of Portland cement. Portland cement has been in widescale use since at least 1850 (Lea, 1971), and apparently was used as the mortar for the Stone Fort. Although raw, wet cement is highly alkaline (pH 11–12), acidic agents in rainwater and in humic substances from decayed plant materials act to neutralize the alkalinity. Our soil samples are neutral (pH 6.96–7.00); these pH values are typical of well-aged wall soils (Segal, 1969).

Results of the sodium and chloride analyses, in μg/g of soil (ppm) are: landward, 250 ppm Na and 110 ppm Cl; seaward, 1200 ppm Na and 280 ppm Cl. The seaward wall soil has nearly five times as much sodium and more than twice as much chloride as the soil from the landward wall, confirming the influence of salt spray on the seaward side.

DISCUSSION

It is uncertain when *A. platyneuron* and *W. obtusa* first appeared in the mortar of the Stone Fort. Little of the mortar remains unweathered, and extensive sections are missing. It is possible that the latter sections once supported populations of the ferns. It cannot be decided on the basis of the available data whether it is the high calcium content or the neutral pH of the soil that accounts for the presence of the ferns; both conditions are uncommon on Long Island.

We inspected herbaria at New York Botanical Garden, Brooklyn Botanic Garden, and Planting Fields Arboretum, and consulted with staff of the New York State Herbarium, Albany. *Woodsia obtusa* has been collected at Ridgewood, in Queens County (*G. B. Brainerd* in 1866, BKL 022985); on rocks near Greenport, in Suffolk County, Long Island (BKL 1862); and in "dry woods" there (*R. Latham* in 1918, NY 824). The Fort Totten collection (*Greller* in 1973, BKL) is the first *Woodsia* from stone walls on Long Island. Edward Frankel (pers. comm.) reports *W. obtusa*

as common on old walls in Westchester County, north of Long Island. *Woodsia* was collected "on walls of old ice chute, south side" at Rockland Lake, Clarkstown Township, Rockland County, New York (*J. H. Lehr* in 1954, NY), also north of Long Island. Jelliffe (1899) listed *A. platyneuron* as "frequent throughout Long Island." Nevertheless, Greller (1977, 1979) did not encounter it in the only remaining extensively forested sites in Queens County: Cunningham, Forest, and Alley Parks. Until they are reported elsewhere, the Fort Totten populations of *W. obtusa* and *A. platyneuron* are the only ones documented in Queens County. Their absence from former terrestrial habitats may be caused by a decrease in soil pH, perhaps as a result of acid rain. Precipitation pH in Queens County since 1970 has averaged about 4.0, monthly averages ranging from 3.5 (summer) to 4.5 (spring and fall) (D. C. Locke, unpubl.).

Occurrence of *W. obtusa* on the seaward wall is noteworthy because of the relatively high levels of sodium and chloride which presumably result from salt spray. Based on salinity measurements made in Hempstead Harbor, a similar bay a few miles east of Fort Totten, the salinity of Long Island Sound at Fort Totten is about 25‰ (D. C. Locke, unpubl.), less than that of ocean water (35‰) but more than sufficient to produce saline spray. The relatively higher level of sodium than chloride in both samples presumably reflects differential leaching of the two elements; according to Lindsay (1979), the level of sodium in soils is typically higher than that of chloride.

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Starch Gel Electrophoresis of Ferns: A Compilation of Grinding Buffers, Gel and Electrode Buffers, and Staining Schedules

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The homosporous pteridophytes have been largely uninvestigated by electrophoresis, despite the fact that they offer many exciting research possibilities (Soltis et al., 1980). The paucity of electrophoretic studies of ferns and fern allies may be due in large part to the high concentrations of condensed tannins that many species contain (Cooper-Driver, 1976 and pers. comm.). These compounds render enzymes inactive by binding with them following cellular disruption, thereby frustrating researchers who have attempted electrophoretic analysis utilizing standard methods of sample preparation.

The method of sample preparation developed by Kelley and Adams (1977a, b) in their analysis of enzyme variation in *Juniperus* was an important procedural breakthrough in overcoming the difficulties that result from the liberation of large amounts of phenolic compounds during tissue preparation. Recently, a simplified version of that method was applied by Soltis et al. (1980) to fern leaf tissue, facilitating rapid preparation of active enzyme samples and thereby making electrophoretic analyses of large numbers of individuals more feasible.

In an attempt to improve methods of analysis of fern enzymes in starch gel electrophoresis, we have experimented with modifications of the method of sample preparation outlined by Soltis et al. (1980). We also have examined several different methods of sample preparation such as those of Gottlieb (1981a), Mitton et al. (1979), and Werth et al. (1982), and have evaluated the relative merits of each with fern tissue. Finally, during the course of our electrophoretic investigations of ferns we found that standard gel and electrode buffers and staining schedules, such as those of Brewer (1970) and Shaw and Prasad (1970), often provided unsatisfactory results when applied to ferns. We have determined gel and electrode buffers, as well as staining schedules, that provide clear starch gel enzyme banding for 22 enzyme systems in ferns. Requests for advice resulting from the recent surge of interest in fern enzyme electrophoresis have prompted us to compile our procedural data so that other researchers can take advantage of our experimentation. We hope that these data will stimulate more extensive electrophoretic investigation of pteridophytes and other electrophoretically difficult taxa.

Gottlieb (1981b) recently reviewed aspects of enzyme electrophoresis primarily in gymnosperms and angiosperms. His discussion is equally relevant to understanding the potential applications and limitations of electrophoretic evidence in pteridophytes. Since homosporous pteridophytes have high chromosome numbers, it is tempting to invoke polyploidy in interpreting their enzyme band patterns. It is well

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TABLE 1. ELECTRODE AND GEL BUFFER RECIPES USED SUCCESSFULLY IN ELECTROPHORETIC ANALYSIS OF FERNS (Gram amounts are given for one liter final volume of buffer except where noted).

Electrode Buffer	pH @ 22°C	*Gel Buffer*	pH @ 22°C
1. 0.400 M Citric Acid, trisodium salt; 117.64 g Citric Acid, trisodium salt dihydrate, 1.0 M HCl to pH 7.0	7.0	0.020 M Histidine·HCl; 4.19 g L-Histidine·HCl monohydrate, 1.0 M NaOH to pH 7.0	7.0
2. 0.135 M Tris, 0.032 M Citric Acid; 16.35 g Tris[a], 6.10 g Citric Acid[b]	8.0	0.009 M Tris, 0.002 M Citric Acid; dilute 67 ml of electrode buffer to 1 liter	8.0[c]
3. 0.135 M Tris, 0.017 M Citric Acid; 16.35 g Tris[a], 3.35 g Citric Acid[b]	8.5	0.009 M Tris, 0.001 M Citric Acid; dilute 67 ml of electrode buffer to 1 liter	8.5[c]
4. 0.223 M Tris, 0.086 M Citric Acid; 27.00 g Tris[a], 16.52 g Citric Acid[b], NaOH to pH 7.5	7.5	0.008 M Tris, 0.003 M Citric Acid; dilute 35 ml of electrode buffer to 1 liter	7.5[c]
5. 0.223 M Tris, 0.069 M Citric Acid; 27.00 g Tris[a], 13.33 g Citric Acid[b]	7.2	0.008 M Tris, 0.002 M Citric Acid; dilute 35 ml of electrode buffer to 1 liter	7.2[c]
6. 0.100 M NaOH, 0.300 M Boric Acid; 4.00 g NaOH, 18.55 g Boric Acid[b]	8.6	0.015 M Tris, 0.004 M Citric Acid; 1.84 g Tris[a], 0.69 g Citric Acid[b]	7.8
7. 0.038 M LiOH, 0.188 M Boric Acid; 1.60 g $LiOH \cdot H_2O$, 11.60 g Boric Acid[b] Adjust to pH 8.3 with dry components	8.3	0.045 M Tris, 0.007 M Citric Acid, 0.004 M LiOH, 0.019 M Boric Acid; Tris-citrate buffer (5.45 g Tris[a], 1.28 g Citric Acid[b], bring volume to 900 ml), add 100 ml electrode buffer to give 9:1 ratio, 1.0 M NaOH to pH 8.3	8.3

8. 0.039 M LiOH, 0.263 M Boric Acid; 1.64 g $LiOH \cdot H_2O$, 16.23 g Boric Acid[b]	8.0	0.042 M Tris, 0.007 M Citric Acid; 0.004 M LiOH, 0.025 M Boric acid; 5.04 g Tris[a], 1.25 g Citric Acid[b], 0.16 g $LiOH \cdot H_2O$, 1.56 g Boric Acid[b], 1.0 M HCl to pH 7.6	7.6 7.6
9. 0.065 M L-Histidine free base, ca. 0.015 to 0.016 M Citric Acid; 10.09 g L-Histidine free base, Citric Acid[b] to pH 5.7 (= ca. 2.9 to 3.1 g)	5.7	0.009 M L-Histidine, 0.002 M Citric Acid; dilute 140 ml of electrode buffer to 1 liter	5.7
10. 0.180 M Tris, 0.004 M EDTA, 0.100 M Boric Acid; 21.80 g Tris[a], 1.52 g EDTA tetrasodium salt dihydrate, 6.18 g Boric Acid[b], Boric Acid to pH 8.6	8.6	0.045 M Tris, 0.001 M EDTA, 0.025 M Boric Acid; dilute 250 ml of electrode buffer to 1 liter	8.6
11. 0.400 M Citric Acid, trisodium salt; 117.64 g Citric Acid, trisodium salt dihydrate, 1.0 M HCl to pH 7.0	7.0	0.005 M Histidine·HCl; 1.05 g L-Histidine·HCl monohydrate, 1.0 M NaOH to pH 7.0	7.0

[a]Trizma-base (Sigma T1503; Sigma T1378 works as well and is much less expensive).
[b]Amounts of Citric Acid and Boric Acid are given in grams of anhydrous free acid per liter.
[c]Check pH of solution after mixing; pH of Tris buffers will change with dilution.

Buffer systems 1 and 11 are from Gottlieb (1981a).
Buffer systems 2 and 3 are modifications of buffer system I of Shaw and Prasad (1970).
Buffer systems 4 and 5 are modifications of buffer system XII of Shaw and Prasad (1970).
Buffer system 6 is from Mitton et al. (1977).
Buffer system 7 is a modification of the buffer system of Gottlieb (1981a).
Buffer system 8 is a modification of the buffer system of Adams and Joly (1980).
Buffer systems 9 and 10 are from Gottlieb (pers. comm.).

known, however, that multiple forms of a given enzyme may be coded by different alleles at a single locus (allozymes) or by genes at more than one locus (isozymes). Furthermore, many standardly assayed plant enzymes have isozymes located in two or more subcellular compartments (e.g., the cytosolic and chloroplastic isozymes of PGI and PGM discussed by Gottlieb, 1981b, 1982—for interpretation of enzyme symbols see *Table 2*). When found in pteridophytes, multiple, subcellularly compartmentalized isozymes should not be misinterpreted as products of duplicated loci resulting from polyploidy.

According to Chapman et al. (1979), attempts to determine the amount of heterozygosity per locus in homosporous pteridophytes are complicated by recombination between homoeologous duplicated loci. An obvious prerequisite to recombination of this kind is the actual presence of such loci. Gastony and Gottlieb (1982) developed a means of demonstrating whether duplicated loci are, in fact, present in pteridophytes. By electrophoretically analyzing sporophytes taken from nature and individual gametophytes grown from spores of these sporophytes, segregational analysis of sporophytic enzyme banding patterns can be conducted. This permits genetic interpretation of parental sporophytic enzyme phenotypes without the time-consuming crossing programs required by total reliance on sporophytic tissue. Use of this methodology enables the investigator to determine whether apparent heterozygosity of sporophytes is coded by alleles at a single locus or by genes at duplicated (homoeologous) loci. Our application of this methodology to several fern genera (e.g., *Athyrium*, *Bommeria*, and *Pellaea)* has demonstrated that the genetic variability observed in these taxa results from allelic diversity and segregation at single, not duplicated, loci.

MATERIALS

Living sporophytes of *Athyrium filix-femina*, *Bommeria ehrenbergiana*, *B. hispida*, *B. pedata*, *B. subpaleacea*, *Botrychium virginianum*, *Ceratopteris thalictroides*, *Cystopteris bulbifera*, *C. dickieana*, *C. fragilis*, *C. laurentiana*, *C. protrusa*, *C. reevesiana*, *C. tennesseensis*, *C. tenuis*, *Isoëtes butleri*, *I. engelmannii*, *Lygodium japonicum*, *Nephrolepis exaltata*, *Ophioglossum engelmannii*, *Pellaea andromedifolia*, *P. atropurpurea*, *P. glabella*, *Polypodium polypodioides*, *P. virginianum*, *Polystichum acrostichoides*, *Pteridium aquilinum*, *Woodsia obtusa*, and *W. oregana* were maintained in greenhouse culture and utilized in this investigation. Living gametophytes representing the species of *Athyrium*, *Bommeria*, *Cystopteris*, *Pellaea* and *Pteridium* listed above were cultured on nutrient agar (Gastony & Haufler, 1976) and also provided material for this study.

GRINDING BUFFER SOLUTIONS

We routinely utilize modifications of either the phosphate grinding buffer–polyvinylpyrrolidone (PVP) solution employed by Mitton et al. (1979), the Tris–maleate grinding buffer–PVP solution of Soltis et al. (1980), or the Tris–HCl grinding buffer–PVP solution of Gottlieb (1981a) with PVP substituted for polyvinylpolypyrrolidone (PVPP), as described below. Recipes for preparing these grinding buffer solutions are provided below; molarity or percent volume values are provided and

gram or milliliter amounts required to prepare 25 ml of buffer solution are given in parentheses.

Phosphate grinding buffer–PVP solution.—0.029 M (0.28 g) sodium tetraborate, 0.017 M (0.08 g) sodium metabisulfite, 0.20 M (1.0 g) L-ascorbic acid sodium salt, 0.016 M (0.07 g) diethyldithiocarbamic acid sodium salt, 4% w/v (1.0 g) PVP average molecular weight 40,000 (Sigma PVP 40T), or 36–40% w/v (9.0–10.0 g) PVP average molecular weight 10,000. Dissolve gram amounts in 25 ml of 0.10 M phosphate buffer pH 7.5 (to make 100 ml of phosphate buffer dissolve 1.36 g KH_2PO_4 in H_2O, add 9.0 ml 1M NaOH, and bring volume to 100 ml with H_2O) and then add 0.25 ml (1%) 2-mercaptoethanol.

Tris–maleate grinding buffer–PVP solution.—0.20 M (1.91 g) sodium tetraborate, 0.02 M (0.095 g) sodium metabisulfite, 0.25 M (1.24 g) L-ascorbic acid sodium salt, 0.026 M (0.113 g) diethyldithiocarbamic acid sodium salt, 0.10 M (0.29 g) maleic acid, 0.10 M (0.30 g) Tris, 4% w/v (1.0 g) PVP average molecular weight 40,000 or 32–40% w/v (8.0–10.0 g) PVP average molecular weight 10,000. For 25 ml of buffer, dissolve amounts indicated in 19 ml distilled water; mix thoroughly and crush out lumps; adjust to pH 7.5 with 1.0 M HCl; add 0.025 ml (0.1%) 2-mercaptoethanol; add H_2O to 25 ml. Originally (when we utilized PVP 10,000) it was necessary to allow the PVP to hydrate overnight before using the grinding buffer solution. When employing PVP 40,000, it is possible to prepare the grinding buffer solution immediately prior to sample preparation by stirring the PVP into solution.

Tris–HCl grinding buffer–PVP solution.—0.1% v/v (0.025 ml) 2-mercaptoethanol, 0.001 M (0.010 g) EDTA (tetrasodium salt), 0.010 M (0.019 g) potassium chloride, 0.010 M (0.050 g) magnesium chloride hexahydrate, 4 or 20% w/v (1 or 5 g) PVP 40,000, 25 ml 0.10 M Tris–HCl buffer, pH 7.5. Stir the PVP into solution or allow it to hydrate in the buffer overnight.

TABLE 2. GEL AND ELECTRODE BUFFER SYSTEMS THAT WE HAVE FOUND TO YIELD THE BEST BANDING IN FERNS WE HAVE ASSAYED.

Enzyme	*Symbol*	*Gel and Electrode Buffer System* (from Table 1)
Acid phosphatase	APH	6, 7
Aconitase	ACN	1, 5, 9
Aldolase	ALD	1–5, 7, 10, 11
Aspartate aminotransferase	AAT (or GOT)	6, 7, 8
Catalase	CAT	4, 7, 8, 10
Esterase (Colorimetric)	EST	6, 7
Esterase (Fluorescent)	FE	8
Fructose-1,6-diphosphatase	F1,6DP	1, 11
Glucose-6-phosphate dehydrogenase	G6PDH	4, 5, 6, 7
Glutamate dehydrogenase	GDH	3, 5, 7
Glyceraldehyde-3-phosphate dehydrogenase	G3PDH	1, 11
Hexokinase	HK	2, 3, 5, 11
Isocitrate dehydrogenase	IDH	1, 2, 3, 4, 5
Leucine aminopeptidase	LAP	3, 7, 8
Malate dehydrogenase	MDH	1, 4, 5, 9
Malic enzyme	ME	7, 10
Peroxidase	PER	2, 7
Phosphoglucoisomerase	PGI	5, 6, 7
Phosphoglucomutase	PGM	3, 5, 6, 7, 8
6-Phosphogluconate dehydrogenase	6-PGD	1, 2, 4, 5
Shikimate dehydrogenase	SkDH	1, 2, 4, 5, 11
Triosephosphate isomerase	TPI	2, 5, 6, 7, 8

Comparison of these three grinding buffer solutions indicates that for most enzymes the staining results are highly comparable. For some enzymes, however, the Tris–HCl–PVP solution seems to improve enzyme band clarity (e.g., PGI, PGM, LAP), while for other enzymes the reverse is true. In *Pellaea andromedifolia*, for example, PGI banding was sharp with the Tris–HCl–PVP solution but was inhibited by the presence of ascorbic acid and sodium tetraborate in the Tris–maleate–PVP buffer. In *Athyrium filix-femina*, however, the Tris–maleate–PVP solution gives superior banding for PGI and one more observable EST locus when compared to the Tris–HCl–PVP solution. The phosphate–PVP solution often resulted in reduced APH activity when compared to the other two grinding buffer solutions.

In working with species of *Asplenium*, Werth et al. (1982) used a method of sample preparation that uses caffeine, but not PVP. Following this technique, equal weights of tissue and caffeine were ground in a 0.1 M HEPES pH 7.0 buffer with 0.2% 2-mercaptoethanol and 0.5% sodium metabisulfite to produce a slurry. We found that for virtually all enzyme systems investigated, the method of Werth et al. provided results roughly comparable to those obtained with grinding buffers containing PVP. The presence of 0.5% sodium metabisulfite in the grinding buffer appears to be of great importance. When this ingredient is omitted from the buffer, activity is noticeably reduced or almost totally lost for many enzymes. Significantly, the full complement of PGI enzyme bands obtained with PVP was not expressed in most of the fern taxa investigated when sodium metabifsulfite was omitted. These results are in agreement with similar observations of Werth et al. (1982).

It should be emphasized that to obtain the best results, the appropriate amount of PVP depends upon the taxon under investigation and in part upon the molecular weight of the PVP employed. Soltis et al. (1980) utilized a grade of PVP with an average molecular weight of 10,000 (although this is not stated in their report) and incorporated 40% w/v PVP (4 g PVP in 10 ml of Tris–maleate grinding buffer). At present, we routinely employ a grade of PVP with an average molecular weight of 40,000. Both molecular weights of PVP are suitable, but less PVP 40,000 is required than PVP 10,000. The amount of PVP used is an important consideration because, as reported by Soltis et al. (1980), use of excessive amounts of PVP in the preparation of grinding buffer-PVP solutions frequently results in a decrease or complete loss of enzyme activity. Although PVPP is effective with a wide range of angiosperms, its substitution for PVP failed to produce banding for PGI in *Pellaea andromedifolia* whether the PVPP was hydrated in the grinding buffer or added directly to the leaf tissue during grinding.

This discussion stresses the importance of selecting optimal grinding buffer components and procedures for the taxon under investigation. As noted above, certain components of these buffers may inhibit band expression, whereas in other cases the full complement of components may be required to obtain clear banding. We have found that LAP activity is greater if sodium ascorbate, sodium tetraborate, and sodium metabisulfite are eliminated from the grinding buffer. On the other hand, activity for some enzymes, (e.g., SkDH, G6PDH, MDH, CAT, 6PGD) may be very noticeably reduced when a buffer solution incorporating only PVP is

utilized. A further complication in some taxa is that when a grinding buffer lacking 2-mercaptoethanol is employed, artifactual ("ghost") bands proliferate for some enzymes and can hinder accurate interpretation of the band patterns. Given these examples, we strongly encourage comparative experimentation with grinding buffer solutions when initiating electrophoretic studies.

SAMPLE PREPARATION AND ELECTROPHORESIS

Leaf samples to be analyzed electrophoretically were taken from mature sporophytes. The methods discussed herein, however, are applicable to gametophytic as well as sporophytic tissue. In our original electrophoretic analyses of ferns, leaf samples were prepared according to the method of Soltis et al. (1980) in which small amounts of leaf tissue are ground under liquid nitrogen with a porcelain mortar and pestle until a fine dry powder is obtained. The powder is quickly mixed with grinding buffer to form a thick slurry. This slurry is absorbed directly into thick paper wicks (made from Whatmann 3 MM chromatography paper or some other suitable wick paper).

It should be emphasized that the use of the grinding buffer–PVP solutions alone (outlined above), without the use of liquid nitrogen in the preparation of samples, provide clear enzyme banding in all of the fern taxa that we have examined so far. Therefore, at present we utilize a simplified method of sample preparation in which liquid nitrogen has been eliminated. In standardizing our grinding procedure by consistently homogenizing 100 mg of leaf material in 0.5 ml of grinding buffer, we obtained roughly equivalent staining intensity for all samples, which facilitates comparing individuals and scoring gels. If small amounts of tissue are being ground, it may be possible to substitute 43 mm^2 plastic weigh boats for mortars and glass or plexiglass rods for pestles. As discussed by Gastony and Gottlieb (1982), it is possible to obtain enzyme banding from single gametophytes. Their technique involves smearing individual gametophytes onto wicks pre-moistened with extraction buffer–PVP solution. With all of the described grinding/extraction procedures, the amount of grinding buffer and the type and size of wicks should be tailored to the taxon and tissues under investigation. Once the plant material has been absorbed into wicks, the wicks are inserted into a vertical slit in the starch gel and subjected to horizontal electrophoresis at 4°C. Band definition may be improved by removing wicks from the gel after the first 10–20 minutes of electrophoresis. It is important to maintain electrical contact across the slit in the gel. We routinely place some sort of spacer (e.g., strips of Whatmann paper, a plastic straw, a thin piece of plexiglass) at the cathodal end of the gel to compress the gel slightly and to insure that the slit does not open.

To permit comparison of banding patterns between gels, it is important to maintain a constant starch concentration throughout a study. We have experimented with a variety of starch concentrations throughout the practical range of 11.5 to 15% and have found concentrations of 12 to 13.2% most suitable, although in some instances alternative concentrations may improve band resolution. Connaught, Fisher, and Sigma starch have been used and all provide clear enzyme banding, provided appropriate gel and electrode buffer systems and staining schedules are utilized.

In order to facilitate determining the location of the anodal front, it is useful to insert a wick bearing the marker dye Bromphenol Blue (Sulfone Form, Sigma B0126; 0.04% w/v in 95% ethanol). Depending on the gel and electrode buffer system employed, as well as the taxon under investigation, the enzyme bands will migrate varying distances behind the Bromphenol Blue marker. Optimal running times for each enzyme system will therefore have to be determined empirically.

GEL AND ELECTRODE BUFFER RECIPES

We have found that standard gel and electrode buffer systems, such as those of Shaw and Prasad (1970), and Brewer (1970), often yield unsatisfactory results with fern tissue. We have determined gel and electrode buffer systems that provide clear banding for 22 enzymes in ferns. Recipes for the gel and electrode buffers we most commonly employ are provided in *Table 1*.

Several of the gel and electrode buffer systems that we employ are modifications of those of Shaw and Prasad (1970). It should be noted, therefore, that errors are present in several of the recipes they provided. For example, in Shaw and Prasad buffer system I (see page 299, Table 1 of their report), utilization of 16.35 g of Tris yields an electrode buffer with a molarity of 0.135 (see present report, *Table 1*, electrode buffers 2 and 3), rather than 0.155 as reported by Shaw and Prasad. Similarly, use of 27.0 g of Tris in the preparation of the electrode buffer of Shaw and Prasad system XII yields a molarity of not 0.233 but 0.223 (see present report, *Table 1*, electrode buffers 4 and 5). Furthermore, use of the electrode buffer recipe of Shaw and Prasad system XII yields a buffer of approximately pH 5.5, which differs significantly from the estimate of pH 7.0 listed by Shaw and Prasad. Use of the amounts of Tris and citric acid given for system 4 in *Table 1* of the present report will also yield an electrode buffer of pH 5.5; sodium hydroxide is then added to adjust the buffer to pH 7.5.

Of the 11 gel and electrode buffer systems for which recipes are provided in *Table 1*, some clearly are preferable to others for certain of the 22 enzymes for which we have obtained sharp banding. For example, best enzyme banding for MDH is obtained when system 1, 4, 5, or 9 is used. Which system works best is dependent, in part, on the taxon under investigation. We have found, for example, that the best systems for *Athyrium* and *Cystopteris* differ somewhat from those that supply clear enzyme banding for *Bommeria*. The systems provided here, however, should provide an excellent framework for conducting electrophoretic analyses of most ferns. The gel and electrode buffer systems that we have found to yield the clearest banding for each of the 22 enzymes with which we have experimented are listed in *Table 2*.

STANDARD STAINING SCHEDULES

During the course of our electrophoretic investigations of ferns, we found that many published staining schedules, such as those of Shaw and Prasad (1970), yielded unsatisfactory results. Enzyme banding often can be improved dramatically when these standard recipes are modified. One very important modification that we employ involves increasing the pH of the buffer in staining schedules for ALD, GDH, G6PDH, HK, IDH, MDH, ME, PGI, PGM, and 6PGD. Tris–HCl staining buffers of pH 7.0 or 7.1 typically are used in staining for these enzymes (Shaw &

Prasad, 1970). We have found, however, that in ferns the pH optima for these enzymes are in the 8.0–8.5 range, and we therefore use a Tris–HCl staining buffer of pH 8.0–8.5 for them. For some enzymes, this simple modification improves staining dramatically. For example, standard MDH staining recipes use a buffer of pH 7.0. Application of such a protocol to ferns, however, often results in very little or inconsistent staining. Well stained bands are obtained consistently for MDH when a Tris–HCl staining buffer of pH 8.0–8.5 is used (provided an appropriate gel and electrode buffer system is employed; see *Table 2*).

It also should be noted that we have consistently been unable to obtain observable activity with fern leaf tissue for some enzymes, despite considerable experimentation. These include Alcohol dehydrogenase, Alkaline phosphatase, α-Glycerophosphate dehydrogenase and Lactate dehydrogenase. There are several enzymes for which we have obtained observable activity with ferns, but have not yet obtained clear banding, such as Diaphorase and Peptidase, and these are therefore not included in this report. In addition, there are a number of enzyme staining schedules that we have not yet attempted. We hope that the staining schedules provided below will stimulate additional experimentation in this regard.

The staining schedules that we utilize for the 22 enzymes for which we obtain clear banding are provided below in alphabetical order. The final volume for all stain recipes is 100 ml. Depending on gel size and staining container capacity, it may be possible to assay two gel slices simultaneously with each of the following 22 solutions. Alternatively, when assaying single gel slices, the recipes may be halved to 50 ml final volume. Readers are encouraged to consult *Enzyme Nomenclature 1978* (International Union of Biochemistry, Nomenclature Committee, 1979 [hereafter referred to as I.U.B., 1979]) for details of enzyme specificity and Gottlieb (1981b) for a recent review of the electrophoretic technique and its application to plant populations. It should be noted that enzymes such as peroxidases, esterases, and acid phosphatases operate on a large number of substrates in vitro; therefore, standard staining protocols for these enzymes result in the staining of various numbers of isozymes whose homologies are not apparent. Although the utility of these isozymes in between-species comparisons is therefore limited, their banding patterns can be useful in assessing variability within populations.

Several different organisms serve as the source for commercial preparations of Glucose-6-phosphate dehydrogenase. This enzyme typically is specific for NADP, but some forms are capable of utilizing either NADP or NAD. It should be emphasized that NADP is much more expensive than NAD, hence selecting a Glucose-6-phosphate dehydrogenase type that can use NAD will save considerable money. Therefore, in those recipes that call for added Glucose-6-phosphate dehydrogenase, the notation NAD(P)* reflects this option.

Acid phosphatase (EC 3.1.3.2)

0.05 M sodium acetate buffer, pH 5.0	100 ml
1.0 M $MgCl_2$	0.5 ml
α-naphthyl acid phosphate, sodium salt	100 mg
Fast garnet GBC salt	80 mg

We have obtained results with buffer molarities ranging from 0.05 M to 0.2 M and within a pH range of 5.0 to 6.0. Stain at room temperature; a modification of

Scandalios (1969). Gottlieb (1981b) noted that plants may have a dozen or more acid phosphatases. We consistently have observed one very intense zone of acid phosphatase activity, with several fainter bands occasionally evident.

Aconitase (EC 4.2.1.3.; = Aconitate hydratase in I.U.B., 1979)

1.0 M Tris-HCl buffer, pH 8.5	10 ml
H_2O	90 ml
cis-aconitic acid	70 mg
Isocitrate (=Isocitric) dehydrogenase	7 units
1.0 M $MgCl_2$	1 ml
NADP	10 mg
MTT	5 mg
PMS	1 mg

Stain in the dark at 30°C; a modification of Shaw and Prasad (1970).

Aldolase (EC 4.1.2.13; = Fructose-biphosphate aldolase in I.U.B., 1979)

1.0 M Tris-HCl buffer, pH 8.5	10 ml
H_2O	90 ml
Fructose-1,6-diphosphate,	
tetra(cyclohexylammonium) salt	500 mg
or	
trisodium salt	200 mg
1.0 M arsenic acid, sodium salt	1 ml
Glyceraldehyde-3-phosphate dehydrogenase	200 units
NAD	20 mg
MTT	20 mg
PMS	5 mg

Stain at room temperature; a modification of Shaw and Prasad (1970).

Aspartate aminotransferase (EC 2.6.1.1.; = Glutamate oxaloacetate transaminase)

1.0 M Tris-HCl buffer, pH 8.0	10 ml
H_2O	90 ml
L-aspartic acid	100 mg
α-ketoglutaric acid	100 mg

Adjust pH to 8.0 with 1.0 M NaOH as necessary, then add:

Pyridoxal-5′-phosphate	5 mg
Fast blue BB salt	100 mg

Stain in the dark at room temperature; a modification of Gottlieb (1973a) and Selander et al. (1971, appendix). Our results show that this enzyme is very sensitive to the pH of the staining buffer; very little staining is observed at pH 7.0 or at pH 9.0. The number of loci coding for proteins that are capable of this aminotransferase reaction is known to vary in plants. Although we typically encounter a single locus, Gottlieb (1981b) has reported the likelihood of specific subcellular localizations for the several dimeric isozymes.

Catalase (EC 1.11.1.6)

3% H_2O_2	5 ml
0.1 M phosphate buffer, pH 7.0	10 ml
0.06 M $Na_2S_2O_3 \cdot 5H_2O$	7 ml
H_2O	78 ml

Incubate in this solution at room temperature for 1–2(30) minutes; pour off the solution, rinse several times with distilled water, then add:

0.09 M KI	50 ml
H_2O	50 ml

Catalase activity will appear as white bands on a dark blue background; a modification of Shaw and Prasad (1970). For some of the buffer systems in *Table 1*, it may be necessary to add several drops (approximately 2 ml) of glacial acetic acid in order to induce staining. An alternative method is to substitute 50 ml 0.05 M sodium acetate buffer (pH 5.0) for the 50 ml H_2O. The gel may turn completely blue in a very short time. Be prepared either to photograph the gel or score it while staining. One locus has been observed in ferns. The protein is reported to be tetrameric (Scandalios, 1969).

Esterase (Colorimetric; EC 3.1.1.–)

α-naphthyl acetate	40 mg
ß-naphthyl acetate	40 mg
dissolved in acetone	2 ml
1.0 M phosphate buffer, pH 6.0	10 ml
H_2O	90 ml
Fast blue RR salt	100 mg

Stain at room temperature; a modification of Gottlieb (1974).

Esterase (Fluorescent; EC 3.1.1.–)

4-methylumbelliferyl acetate	42 mg
dissolved in acetone	25 ml
1.0 M sodium acetate buffer, pH 5.0	18 ml
H_2O	57 ml

Stain in the dark at room temperature and observe under long-wave ultraviolet light; staining schedule of Mitton et al. (1979). Observe immediately after staining (bands fade quickly). Caution should be exercised in scoring gels because flavonoid "bands" may also be visualized under UV light. To determine whether flavonoid "bands" are present, the gel slice should be observed under UV light prior to staining.

Fructose-1,6-diphosphatase (EC 3.1.3.11; =Fructose-biphosphatase in I.U.B., 1979)

1.0 M Tris-HCl buffer, pH 8.0	10 ml
H_2O	90 ml
Fructose-1,6-diphosphate,	
tetra(cyclohexylammonium) salt	250 mg
or	
trisodium salt	100 mg
1.0 M $MgCl_2$	1 ml
Phosphoglucoisomerase	50 units
Glucose-6-phosphate dehydrogenase	50 units
NAD(P)*	10 mg
MTT	5 mg
PMS	1 mg

Stain in the dark at 30° C; a modification of Shaw and Prasad (1970).

Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)

1.0 M Tris-HC1 buffer, pH 8.0 or 8.5	10 ml
H_2O	90 ml
Glucose-6-phosphate, disodium salt	100 mg
NADP	20 mg
MTT (or NBT)	10 mg
PMS	2 mg

Stain in the dark at 37° C; a modification of Shaw and Prasad (1970).

Glutamate dehydrogenase (EC 1.4.1.2)

1.0 M Tris-HC1 buffer, pH 8.0	10 ml
H_2O	70 ml
1.0 M L-glutamic acid, pH 8.0 (use free acid or monosodium salt and add NaOH to pH 8.0)	20 ml
NAD	20 mg
MTT (or NBT)	10 mg
PMS	2 mg

Stain in the dark at room temperature; a modification of Gottlieb (1973b) and of Shaw and Prasad (1970).

Glyceraldehyde-3-phosphate dehydrogenase (EC 1.2.1.12; = Glyceraldehyde-phosphate dehydrogenase in I.U.B., 1979)

1.0 M Tris-HC1 buffer, pH 8.0	10 ml
H_2O	90 ml
Fructose-1,6-diphosphate, trisodium salt	100 mg
Aldolase	10 units

Incubate above mixture approx. 30 min. at 30–37° C, then add:

1.0 M arsenic acid, sodium salt	1 ml
NAD	10 mg
MTT	5 mg
PMS	1 mg

Stain in the dark at 30° C; a modification of Shaw and Prasad (1970).

Hexokinase (EC 2.7.1.1)

1.0 M Tris–HCl buffer, pH 8.5	10 ml
H_2O	90 ml
Glucose	90 mg
1.0 M $MgCl_2$	5 ml
EDTA, tetrasodium salt, dihydrate	40 mg
NAD(P)*	10 mg
MTT (or NBT)	15 mg
Glucose-6-phosphate dehydrogenase	40 units
PMS	2 mg
ATP	25 mg

Stain in the dark at room temperature; a modification of Shaw and Prasad (1970).

Isocitrate dehydrogenase [$NADP^+$] (EC 1.1.1.42)

1.0 M Tris–HC1 buffer, pH 8.0	10 ml
H_2O	85 ml
Isocitric acid, trisodium salt	100 mg
1.0 M $MgCl_2$	5 ml
NADP	10 mg

MTT (or NBT)	15 mg
PMS	2 mg

Depending on the taxon being analyzed, results have been obtained by using buffers ranging from pH 7.2 to pH 8.5. Stain in the dark at room temperature; a modification of Shaw and Prasad (1970).

Leucine aminopeptidase (EC 3.4.11.–)

L-leucine-β-naphthylamide (free base or acid salt) dissolved in dimethyl formamide	20 mg 5 ml
1.0 M phosphate buffer, pH 6.0	10 ml
H_2O	90 ml
Black K salt or fast black K salt	50 mg

Stain in the dark at room temperature; a modification of Gottlieb (1973c). This enzyme has broad activity; it can cleave a number of N-terminal amino acids. Although commonly referred to as Leucine aminopeptidase ("LAP"), it is more precisely referred to as Aminopeptidase. There are a number of aminopeptidases, some of which are specific for certain N-terminal amino acids. Aminopeptidase (cytosol; EC 3.4.11.1) is activated by heavy metals, whereas Aminopeptidase (microsomal; EC 3.4.11.2) is not activated by heavy metals (I.U.B., 1979). It may be necessary to modify the pH of the stain in order to increase staining intensity. One isozyme is usually observed and a second is occasionally apparent; both are monomeric.

Malate dehydrogenase (EC 1.1.1.37)

1.0 M Tris-HC1 buffer, pH 8.0 or 8.5	10 ml
2.0 M DL-malic acid, pH 8.0 (add NaOH to pH 8.0)	10 ml
H_2O	80 ml
NAD	10 mg
MTT (or NBT)	10 mg
PMS	2 mg

Stain in the dark at room temperature; a modification of Shaw and Prasad (1970). Some investigators add 38 mg EDTA (tetrasodium salt, dihydrate) to this recipe. We use 2.0 M DL-malic acid rather than 1.0 M L-malic acid as most standard staining schedules require because DL-malic acid is much less expensive than purified L-malic acid, which is the actual substrate. There are at least four malate NAD^+ dehydrogenases reported (I.U.B., 1979). The one most frequently reported in routine electrophoresis is L-Malate: NAD^+ oxidoreductase (EC 1.1.1.37), of which at least two putative isozymes have been observed. The protein is dimeric; subcellular compartmentalization of the isozymes is discussed by Gottlieb (1981b).

Malic enzyme (EC 1.1.1.40; = Malate dehydrogenase [Oxaloacetate-decarboxylating, $NADP^+$] in I.U.B., 1979)

1.0 M Tris-HC1 buffer, pH 8.0 or 8.5	10 ml
H_2O	80 ml
2.0 M DL-malic acid, pH 8.0 (prepare as in Malate dehydrogenase)	10 ml
1.0 M $MgC1_2$	2 ml
NADP	20 mg
MTT (or NBT)	20 mg
PMS	2 mg

Stain in the dark at room temperature; a modification of Richmond (1972 and pers. comm.).

Peroxidase (EC 1.11.1.7)

3-amino-9-ethyl carbazole	65 mg
dissolved in dimethyl formamide	5 ml
0.05 M sodium acetate buffer, pH 5.0	95 ml
0.1 M $CaCl_2$	2 ml
3% H_2O_2	2 ml

Incubate the gel in a refrigerator until the bands appear (30–60 min); a modification of Shaw and Prasad (1970) and of Gottlieb (1973b).

Phosphoglucoisomerase (EC 5.3.1.9; = Glucosephosphate isomerase in I.U.B., 1979)

1.0 M Tris–HCl buffer, pH 8.0	10 ml
H_2O	90 ml
1.0 M $MgCl_2$	1 ml
Fructose-6-phosphate, disodium salt	30 mg
Glucose-6-phosphate dehydrogenase	40 units
NAD(P)*	10 mg
MTT (or NBT)	20 mg
PMS	2 mg

Stain in the dark at 37°C or at room temperature; a modification of Shaw and Prasad (1970). This dimeric enzyme has numerous synonyms (I.U.B., 1979) including: Phosphohexose isomerase, Phosphohexomutase, Oxoisomerase, Hexose phosphate isomerase, Glucose-6-phosphate isomerase, Phosphosaccharomutase, and Phosphohexoisomerase. Cytosolic and chloroplastic isozymes should be expected (Gottlieb, 1981b, 1982).

Phosphoglucomutase (EC 2.7.5.1)

1.0 M Tris–HCl buffer, pH 8.0 or 8.5	10 ml
H_2O	90 ml
1.0 M $MgCl_2$	2 ml
Glucose-1-phosphate, disodium (Sigma G7000) or dipotassium (Sigma G6875) salt	100 mg
1.7×10^{-4} M α-D-glucose-1,6-diphosphate, tetra(cyclohexylammonium) salt	5 ml
Glucose-6-phosphate dehydrogenase	40 units
NAD(P)*	10 mg
MTT (or NBT)	20 mg
PMS	2 mg

A modification of Shaw and Prasad (1970). An equally suitable alternate recipe which eliminates the need to purchase α-D-glucose-1,6-diphosphate is:

1.0 M Tris–HCl buffer, pH 8.0	10 ml
H_20	90 ml
1.0 M $MgCl_2$	2 ml
Glucose-1-phosphate, disodium salt (Sigma G1259)	50 mg
Glucose-6-phosphate dehydrogenase	40 units
NAD(P)*	10 mg
MTT	10 mg
PMS	2 mg

Stain in the dark at 37°C or at room temperature.

6-Phosphogluconate dehydrogenase (EC 1.1.1.44)

1.0 M Tris–HC1 buffer, pH 8.0	10 ml
H_2O	90 ml
6-phosphogluconic acid, barium salt	40 mg
1.0 M $MgCl_2$	2 ml
NADP	10 mg
MTT	10 mg
PMS	2 mg

Stain in the dark at room temperature or at 37°C; a modification of Shaw and Prasad (1970).

Shikimate dehydrogenase (EC 1.1.1.25)

1.0 M Tris–HC1 buffer, pH 8.5	10 ml
H_2O	90 ml
Shikimic acid	100 mg
NADP	10 mg
MTT (or NBT)	20 mg
PMS	2 mg

Stain in the dark at room temperature or at 37°C.

Triosephosphate isomerase (EC 5.3.1.1)

1.0 M Tris-HC1 buffer, pH 8.0	10 ml
H_2O	90 ml
Dihydroxyacetone phosphate, lithium salt	10 mg
EDTA, tetrasodium salt, dihydrate	38 mg
NAD	30 mg
MTT	10 mg
PMS	2 mg
Arsenic acid, sodium salt	460 mg
Glyceraldehyde-3-phosphate dehydrogenase	300 units

Stain in the dark at 37°C; Gottlieb (pers. comm.). An alternative and much less expensive method of staining for TPI follows (also see agarose recipe):

1.0 Tris–HC1 buffer, pH 8.0	10 ml
H_2O	90 ml
DL-α-glycerophosphate	200 mg
Pyruvic acid, sodium salt	100 mg
α-Glycerophosphate dehydrogenase	100 units
Lactate dehydrogenase	100 units
NAD	20 mg

Incubate the above solution for 2 hours at 30–37°C. At the end of the incubation period, inactivate the enzymes by adjusting the solution to pH 2.0 with 1.0 M HC1 (taking care not to go below pH 2.0) and then re-adjust to pH 8.0 with 1.0 M NaOH. Add:

1.0 M arsenic acid, sodium salt	1 ml
Glyceraldehyde-3-phosphate dehydrogenase	100 units
NAD	20 mg
MTT	5 mg
PMS	1 mg

Stain in the dark at 30°C. The bands will be dark blue on a light blue background. Readers who follow this protocol must first show the lack of α-Glycerophosphate dehydrogenase activity in their taxa. This can be done simply by staining a gel slice with:

1.0 M Tris-HCl buffer, pH 8.0	10 ml
H_2O	90 ml
DL-α-glycerophosphate	200 mg
NAD	20 mg
MTT	5 mg
PMS	1 mg

AGAROSE STAINING SCHEDULES

Several of the reagents commonly required in enzyme electrophoresis, such as NADP, are expensive. Costs may be reduced by using staining schedules employing agarose (modified from Mitton et al., 1979 and Gaines, pers. comm.), which require much smaller quantities of most ingredients than do standard staining schedules but yield comparable results.

Agarose staining schedules are provided below for ALD, G6PDH, GDH, IDH, MDH, PGI, PGM, 6-PGD, SkDH, and TPI. The following general procedure is employed to stain one starch gel slice using the agarose technique: dissolve all ingredients required for enzyme staining (see below) in 6 ml of Tris–HCl buffer; in a second flask mix 0.06 g agarose (Agarose type II, Sigma A6877) with 6 ml distilled water (a 1% agarose solution) and bring this solution to a boil while stirring constantly; combine the two solutions and very quickly apply to surface of one gel slice (it may be necessary to increase ml amounts of buffer and 1% agarose depending on the size of the gel slice); stain all slices in the dark at room temperature.

Aldolase (EC 4.1.2.13)

PMS	1 mg
MTT	5 mg
NAD	10 mg
Fructose-1,6-diphosphate, trisodium salt or tetra(cyclohexylammonium) salt	75 mg
Arsenic acid	25 mg
Glyceraldehyde-3-phosphate dehydrogenase	40 units
0.1 M Tris-HCl buffer, pH 8.5	6 ml
1% agarose	6 ml

Glucose-6-phosphate dehydrogenase (EC 1.1.1.49)

PMS	1 mg
MTT	4 mg
NADP	4 mg
EDTA, tetrasodium salt, dihydrate	6 mg
Glucose-6-phosphate, disodium salt	5 mg
0.1 M Tris–HCl buffer, pH 8.0	6 ml
1% agarose	6 ml

Glutamate dehydrogenase (EC 1.4.1.2)

PMS	1 mg
MTT	4 mg
NAD	3 mg
L-glutamic acid, monosodium salt	100 mg
0.1 M Tris–HCl buffer, pH 8.0	6 ml
1% agarose	6 ml

Isocitrate dehydrogenase [$NADP^+$] (EC 1.1.1.42)

PMS	1 mg
MTT	4 mg
NADP	4 mg
$MgCl_2$	40 mg
Isocitric acid, trisodium salt	10 mg
0.1 M Tris–HCl buffer, pH 8.0	6 ml
1% agarose	6 ml

Malate dehydrogenase (EC 1.1.1.37)

PMS	2 mg
MTT	7 mg
NAD	7 mg
L-malic acid	16 mg
0.25 M Tris–HCl buffer, pH 8.6	6 ml
1% agarose	6 ml

Keep PMS and L-malic acid powders separate until adding the buffer.

Phosphoglucoisomerase (EC 5.3.1.9)

PMS	1 mg
MTT	4 mg
NAD(P)*	1 mg
0.1 M Tris–HCl buffer, pH 8.0	4 ml
10% $MgCl_2$	1 ml
0.018 M fructose-6-phosphate, disodium salt	1 ml
Glucose-6-phosphate dehydrogenase	10 units
1% agarose	6 ml

Phosphoglucomutase (EC 2.7.5.1)

PMS	1 mg
MTT	5 mg
NAD(P)*	4 mg
0.1 M Tris–HCl buffer, pH 8.0	2 ml
0.05 M glucose-1-phosphate, disodium salt (Sigma G7000)	2.5 ml
Glucose-6-phosphate dehydrogenase	10 units
0.001 M fructose-1,6-diphosphate, trisodium salt	1 ml
10% $MgCl_2$	1 ml
1% agarose	6 ml

6-Phosphogluconate dehydrogenase (EC 1.1.1.4.4)

PMS	1 mg
MTT	4 mg
NADP	4 mg
6-phosphogluconic acid, barium salt	10 mg
10% $MgCl_2$	0.5 ml
0.1 M Tris–HCl buffer, pH 8.5	5 ml
1% agarose	6 ml

Dissolve the 6-phosphogluconic acid barium salt in 1.0 ml of 0.1 M Tris–HCl buffer (pH 8.5) approximately 15 minutes before mixing in other ingredients.

Shikimate dehydrogenase (EC 1.1.1.25)

PMS	1 mg
MTT	4 mg
NADP	4 mg
Shikimic acid	10 mg
0.1 M Tris–HC1 buffer, pH 8.0	6 ml
1% agarose	6 ml

Triosephosphate isomerase (EC 5.3.1.1)

PMS	1 mg
MTT	4 mg
NAD	10 mg
EDTA, tetrasodium salt, dihydrate	10 mg
Arsenic acid	150 mg
Dihydroxyacetone phosphate	1.5 mg
Glyceraldehyde-3-phosphate dehydrogenase	75 units
0.1 M Tris–HC1 buffer, pH 8.0	6 ml
1% agarose	6 ml

GEL FIXATION AND DOCUMENTATION

AAT and PER gel slices are fixed in 50% glycerol; all other gel slices are fixed in 50% ethanol.

In order to keep a permanent record of results, we routinely photograph gel slices using Kodak Technical Pan Film 2415 following the exposure index and developing procedure recommended for high contrast.

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SHORTER NOTES

A NEW COMBINATION IN ASPLENIUM.—A new fern was recently added to the flora of Alabama with the naming of the backcross hybrid ×*Asplenosorus boydstonae* Walter (Amer. Fern J. 72:62. 1982.). The type material was collected in Hale County, Alabama, in a locality famous for its fertile alloploid population of Scott's Spleenwort, which arose through hybridization of the Walking Fern and the Ebony Spleenwort. The new hybrid has Scott's Spleenwort and the Ebony Spleenwort as its parents. If the view is held that the Walking Fern belongs in the genus *Asplenium* rather than *Camptosorus*, the "hybrid genus" ×*Asplenosorus* is taxonomically superfluous. The new hybrid then needs to be placed in *Asplenium* and the epithet corrected in conformity with Art. 73.10 of the "International Code of Botanical Nomenclature":

Asplenium ×boydstoniae (Walter) Short, comb. nov.

×*Asplenosorus boydstonae* K. S. Walter, Amer. Fern J. 72:62. 1982. TYPE: Havana Glen, Hale Co., Alabama, *Wagner & Walter 70011* (MICH not seen).

John W. Short, 217 Cook St., Auburn, AL 36830.

ADIANTUM FURCATUM AND MICROSTAPHYLA FURCATA.—The island of St. Helena, outside the Gulf of Guinea off the west coast of Africa, is not only famous because it was the residence in exile of Napoleon Bonaparte. It has also produced a fern, *Microstaphyla bifurcata*, which stands out of proportion when its diminutive size (ca. 10–20 cm) is compared with the long list of names it has been called. Since the establishment of the genus *Microstaphyla* in 1851, it has been placed in no fewer than nine genera! The last revisionary treatment of *Microstaphyla* was by Maxon (J. Washington Acad. Sci. 13:28–31. 1923), who included among the synonyms the name *Adiantum furcatum* L. f. In the "Index Filicum," Christensen (1905) accepted that epithet as *Elaphoglossum furcatum* (L. f.) Christ. That basionym also accounts for the citation *Microstaphyla furcata* (L. f.) Presl, which has been used by some authors, including Maxon, who have overlooked Presl's explicit citation of *Osmunda bifurcata* Jacq. as the basionym of his combination.

In any event, accepting *A. furcatum* as a synonym for the sole species of *Microstaphyla* is an error which originated when the younger Linnaeus included a citation from Plukenet's "Mantissa," "*Filicula corniculata insula Helenae.*" Although Plukenet's polynomial indeed corresponds to *M. bifurcata*, it was erroneously interpreted by the younger Linnaeus to be the same as his *A. furcatum* (Sp. Pl. Suppl. 447. 1881), a plant he reported as "*in Cap. Bonae Spei et insula Helenae.* Thunberg. Thouin." Although Thunberg collected in the Cape and Thouin in Reunión, neither of them set foot on St. Helena, where *Microstaphyla* is endemic. Furthermore, *A. furcatum* is not an *Adiantum* at all, but is *Asplenium achilleifolium* (Lam.) C. Chr. (syn. *A. rutaefolium* (Berg.) Kunze). For this reason, the Linnaean epithet should be deleted as a synonym of *M. bifurcata* (Jacq.) Presl, the correct name.—*Luis Diego Gómez P., Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

NOTEWORTHY PTERIDOPHYTE RECORDS FOR NEBRASKA.—Field studies in the Niobrara River Valley of north-central Nebraska during the summer of 1982 yielded several significant finds. Field work was carried out in connection with a floristic survey of the 54,000-acre Niobrara Valley Preserve, owned by The Nature Conservancy, and in areas peripheral to the Preserve.

Botrychium matricariifolium A. Br. was collected for the first time in Nebraska. In the Great Plains it is otherwise known only from Custer County, South Dakota (Brooks, R. E. Amer. Fern J. 70:91. 1980) and from Lac Qui Parle County, Minnesota (Atlas of the Flora of the Great Plains, Iowa State Univ. Press. 1977). Three plants were observed in a juniper-oak woodland on the south side of the Niobrara River about 15 miles NNE of Johnstown, Brown County. The plants were growing in a sandy, partially shaded soil along the floodplain of the river close to an access road to a center-pivot irrigation pump along the river. Much of the area had been cleared for the road and for an irrigation pipe up a steep, north-facing slope. No additional plants were found during subsequent searches. The plants were photographed and, after the fronds senesced, collected (*Freeman 1517*, KANU).

Ophioglossum vulgatum var. *pseudopodum* (Blake) Farw. was first collected in Nebraska in 1913 by J. M. Bates in the vicinity of Kennedy, Cherry County. Clausen (Mem. Torrey Bot. Club 19:126. 1938) cited the specimen without infraspecific reference; Brooks (Amer. Fern J. 70:92. 1980) referred it to var. *pseudopodum*. A thriving population was found on the south side of the Niobrara River ca. 55 yds east of the Berry Bridge, 5 miles west and 3 miles south of Sparks, Cherry County. The plants covered an area of about 7 × 2 yds at the west end of a beaver pond. They were growing in wet, loamy soil at the edge of a paper birch forest along with *Cicuta bulbifera*, *Onoclea sensibilis*, and *Thelypteris palustris*. The area showed obvious signs of human manipulation, as a dike situated between the river and the west end of the pond was fitted with a pipe to supplement water in the pond during dry periods, possibly as part of a fish hatchery built many years ago. Photographs were taken and voucher specimens (*Freeman & Churchill 1672*) were distributed to various herbaria, including KANU, KSC, NEB, and NY.

Dryopteris carthusiana (Villars) H. P. Fuchs was collected around the turn of the century in Brown, Cass, Cherry, Lancaster, and Thomas counties in Nebraska (A. J. Petrik-Ott, Beih. Nova Hedw. 61:141. 1979). Field studies conducted by a number of researchers in 1980 resulted in the discovery of one population along Little Cedar Creek Canyon in Cherry County (*Sutherland, Boner, Lamp & Joern 5053*, NEB; *Sutherland & Harrison 5314*, NEB). During the course of our survey, we found four populations, all in rich paper birch forests along spring-fed canyons on the south side of the river. Two populations were in Cherry County. One was photographed and collected along Little Cedar Creek Canyon, 5.2 miles south of Sparks (*Freeman & Churchill 1200*, KSC, NEB). A second was just east of Smith Falls, 3 miles east and 4 miles south of Sparks (*Churchill & Brogie 12424*, NEB). The latter was the largest of the populations. Two populations were found in Brown County. One was along Dutch Creek Canyon, 16 miles north of Ainsworth (*Churchill 12300*, NEB). The second was in Kantak Coulee, 3 miles west of Meadville (*Churchill 12408*, NEB).

We wish to thank Dr. W. H. Wagner, Jr. and Ralph Brooks for verifying the specimen of *Botrychium* and Dr. T. M. Barkley and Ralph Brooks for reviewing the manuscript.—*Craig C. Freeman, Division of Biology, Kansas State University, Manhattan, KS 66506* and *Steven P. Churchill, Division of Biological Sciences, University of Kansas, Lawrence, KS 66045*.

SPREAD OF MARSILEA QUADRIFOLIA IN MCDONOUGH COUNTY, ILLINOIS.—Thirty-five years ago Myers found *Marsilea quadrifolia* L. in Spring Lake, McDonough County, Illinois. It is of interest to record how much this alien, potentially weedy plant has spread in that time. Myers (Amer. Fern J. 40:256. 1950) stated that during the years following 1947 *Marsilea* did not become abundant, but he did recognize that it "has persisted following partial draining of the lake, dredging, and a considerable increase in the water level when a higher dam was built" (Annotated Catalogue and Index for the Illinois Flora. Western Illinois Univ. Ser. Biol. Sci. 10:58. 1972). At present, the plant has not spread much in the lake and is still not abundant. Water from the lake flows downstream via Spring Creek for about 4.3 miles where it enters the LaMoine River, which is a tributary of the Illinois River. In 35 years, *M. quadrifolia* has migrated down Spring Creek only one mile. The quantity and distribution of the plants vary, progressing from many plants in the upper part of the creek below the lake and dam to a very few, widely scattered plants beyond one-half mile to finally one plant one mile downstream. The plants are usually at the edge of the creek, particularly near the lake, but further downstream are found characteristically in small "cut-offs" at the edge of the creek. Downstream migration of *Marsilea* has not been rapid, which seems surprising considering the numerous times it could have been dispersed by propagules (including rafts of vegetation), especially during the rush of high waters in spring and fall. Obviously, this non-native plant has not been highly aggressive here in its spread or migration in the lake or creek, although there is little or no apparent competition from other plants and there seem to be many suitable locations for its establishment. Myers (Amer. Fern J. 40:256. 1950) stated that his identifications were made from sterile material, but numerous sporocarps can be found on plants in the lake as well as on plants in the creek up to one-half mile below the lake. The few scattered plants in the next half-mile were sterile. Since this species is about three miles from the LaMoine River (and a brief survey of the LaMoine River particularly downstream from the mouth of Spring Creek indicated no plants present), it seems that if present conditions continue along with the present rate of migration (about 151 feet per year) the prospect for *M. quadrifolia* being a serious weed in the LaMoine-Illinois River system is remote for the near future.—*R. D. Henry, R. M. Myers Herbarium, Western Illinois University, Macomb, IL 61455*.

WOOD FERNS NEW TO MARYLAND AND DELAWARE.—While collecting specimens for Towson State University, I discovered four plants of the Crested Log Fern Hybrid, *Dryopteris celsa* × *cristata*, growing as a fairy ring near Creswell, Harford County, Maryland (*Redman 3541*, BALT, MICH). This discovery represents the fifth state known for this rare hybrid, the closest known locality being about 150 miles northeast in northeastern New Jersey. The plants grew on alluvial soils derived from the James Run gneiss formation in a Beech–Oak woods. The parents were not growing nearby; *D. celsa* is known from 5 miles away and *D. cristata* from 7 miles away. Unfortunately, the hybrids' locality is being destroyed for development, but the plants have been moved into cultivation. I am indebted to Drs. Warren and Florence Wagner for verifying the identity of the specimens.

I also discovered three plants of Miss Slosson's Hybrid Woodfern, *D.* ×*slossonae* Wherry (*D cristata* × *marginalis*), near Kenton, Kent County, Delaware (*Redman 2814*, BALT). The habitat is alluvial woods under a canopy of oak trees. Plants of both parents grow nearby. Apparently this is the first record for this hybrid in Delaware.—*Donn E. Redman, 2615 Harwood Road, Baltimore, MD 21234.*

A NEW COMBINATION FOR AN ASPLENOSORUS HYBRID.—Traditionally, the Walking Fern has been segregated from the spleenworts (*Asplenium*) as *Camptosorus rhizophyllus* (L.) Link. A number of pteridologists, however, question the distinction, pointing out the morphological similarity of Walking Fern to *Asplenium*, its comparable diploid chromosome number ($n = 41$), its preference for rock substrates, and its northeastern distribution. A close alliance with the spleenworts is further demonstrated by its tendency to cross with representatives of the genus *Asplenium* to produce sterile hybrids, some of which have become fertile through chromosome doubling and now behave as distinct species. In the Appalachian Mountains such hybridization and ploidy level changes have led to an extensive allopolyploid complex which has undergone considerable study. Those who maintain the Walking Fern in *Camptosorus* place hybrids with *Asplenium* and their derivatives in the hybrid genus *Asplenosorus*. Most of the hybrids were originally described as spleenworts, and therefore have combinations available under *Asplenium*. One new Walking Fern–Spleenwort hybrid, however, was recently described as an *Asplenosorus*. Its incorporation into the genus *Asplenium* may be accommodated by the following combination:

Asplenium ×shawneense (R. C. Moran) H. E. Ballard, comb. nov.

Asplenosorus ×shawneensis R. C. Moran, Amer. Fern J. 71:85, 1981.

This is the hybrid of *Asplenium rhizophyllum* and *A. trichomanes*, and is known so far only from southern Illinois.—*Harvey E. Ballard, Jr., Department of Biology, Western Michigan University, Kalamazoo, MI 49008.*

AMERICAN FERN JOURNAL

Terry R. Webster, of the Biological Sciences Group, University of Connecticut, Storrs, CT 06268, has been appointed to the editorial staff of the JOURNAL. Professor Webster is a morphologist. His special interest is the morphology and reproductive biology of *Selaginella*. He will be taking on some manuscript reviewing and proofreading duties that are so necessary to the functioning of the JOURNAL. —*D.B.L.*

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AMERICAN FERN JOURNAL

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Vittaria Gametophytes Discovered in a New Physiographic Province

ALLISON W. CUSICK*

Since their recognition over 20 years ago, knowledge of the distribution and taxonomic affinities of the perennial *Vittaria* gametophytes found in the eastern United States has expanded greatly. Once thought to be extremely rare and local, they now are known to be common in selected habitats over a broad region of the Appalachians. Farrar (1978) summarized the history of this taxon and presented a map of its distribution as then understood. *Vittaria* gametophytes have been discovered in the unglaciated Appalachian Plateau, Blue Ridge, Ridge and Valley, and Upland Piedmont provinces, all uplifted bedrock areas which presumably have been in continuous existence since Tertiary times. Farrar et al. (1983) discussed these recent finds and reported the gametophytes from sites in Ohio and Pennsylvania near the limits of Pleistocene glaciation. This article describes the presence of *Vittaria* gametophytes beyond these limits. This unusual fern now has been discovered on the glaciated Appalachian Plateau nearly 90 km north of the southern limit of Wisconsinan glaciation. This also is the first report of *Vittaria* gametophytes from the watershed of the Great Lakes.

The *Vittaria* gametophytes were found 10 June 1982 on Little Mountain, Geauga and Lake counties, Ohio, on property of the Holden Arboretum, Mentor, Ohio (*Fig. 1*). Accompanying the author were Brian Parsons and Thomas Yates, field naturalists of the Arboretum, and Robert McCance of the Division of Natural Areas and Preserves, Ohio Department of Natural Resources. To say that we were surprised by this discovery would be an understatement. Only a small collection was made at this time (*Cusick 21673*, ISC). The author revisited the site on 24 August, searching more thoroughly for gametophytes, and again preparing a voucher (*Cusick 22000*, OS). Colonies of *Vittaria* were found to occur discontinuously in a linear band over approximately 0.5 km of the slope of Little Mountain. Identity of the gametophytes was verified by Dr. Donald R. Farrar of Iowa State University.

The site of this discovery is an extraordinary area not at all typical of glaciated Ohio and a habitat highly suitable for the growth of *Vittaria*. Little Mountain is at the extreme edge of the glaciated Appalachian Plateau, being one of the localized bedrock exposures that mark the escarpment between the elevated Plateau and the Lake Plains of the Central Interior Lowlands province. The mountain is shaped roughly like a dumbbell, oriented north to south, with knobs at either end. The northern knob rises to 380 m, the southern knob to 386 m. Between these summits is a flattened saddle only slightly lower in elevation. The northern knob lies partly in Concord Township, Lake County, while the bulk of the mountain is in Chardon Township, Geauga County. The shoreline of Lake Erie is only 6.5 km north of the mountain. The approximate mean elevation of the lake at that point is 174 m. Thus,

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*Division of Natural Areas and Preserves, Ohio Department of Natural Resources, Fountain Square, Columbus, OH 43224.

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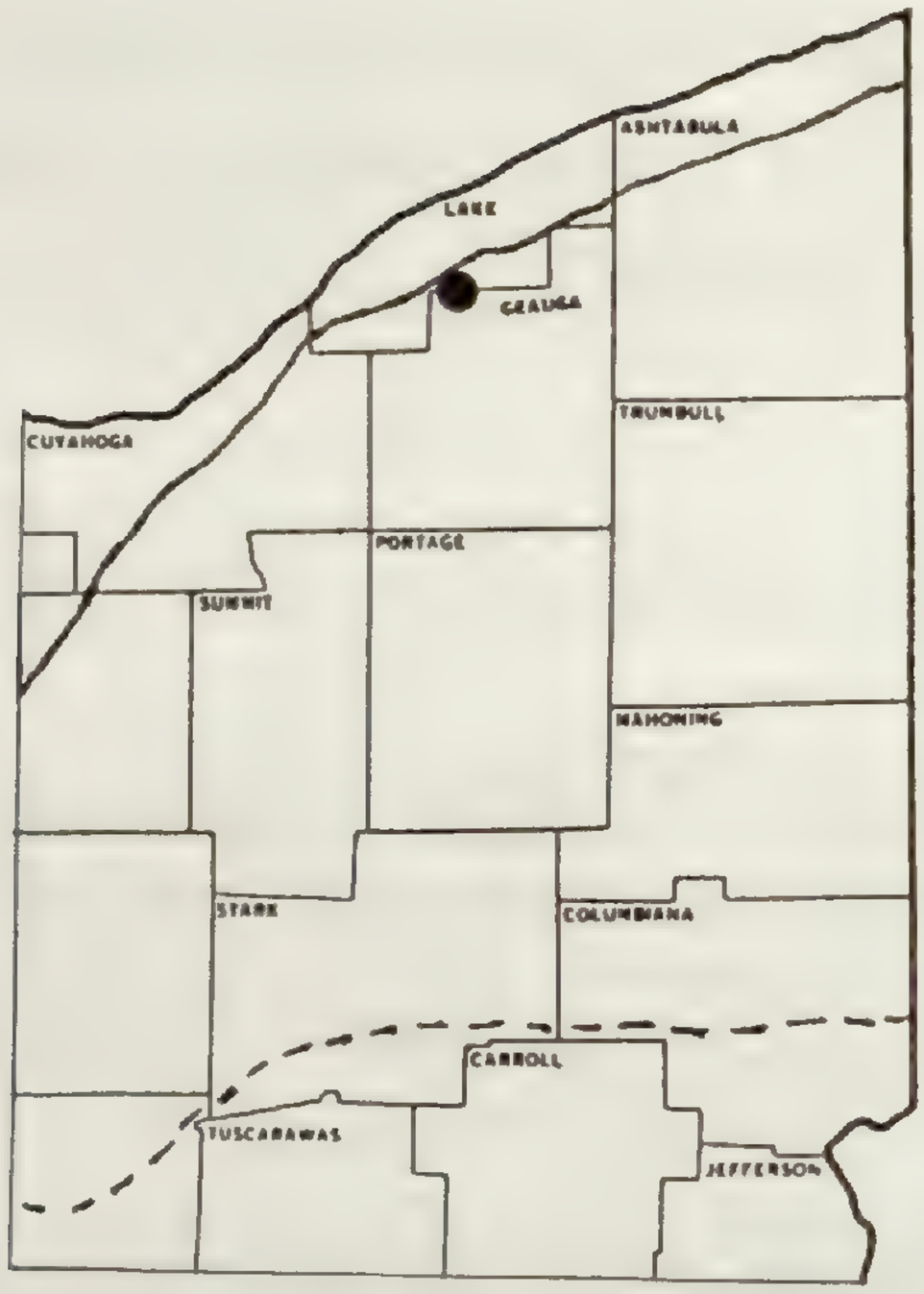

FIG. 1. The northeastern quarter of Ohio. Solid line indicates the northern limit of the glaciated Appalachian Plateau; dashed line, the southern limit of Wisconsinan glaciation. Solid dot is location of Little Mountain.

there is a difference in elevation of 206 m between the mountain and Lake Erie (U.S. Geological Survey, 1970.)

This dramatic change in elevation between lake and summit has a significant effect on local weather patterns. Winds moving south across Lake Erie pick up moisture which is quickly lost once this escarpment is reached. In the lee of these summits, then, is the locally-famous "snow belt" of northeastern Ohio. This local phenomenon is clearly shown on the snowfall map in Gordon (1969) on which the site of Little Mountain may be seen in the pattern of isopleths. Snowfall in the Little Mountain region averages nearly 3 m yearly, far in excess of Ohio's annual average snowfall of about 1 m.

The summits of Little Mountain and the other elevations at the edge of the glaciated Appalachian Plateau in Ohio are capped by the Sharon Conglomerate formation of the Pottsville group of the Pennsylvanian System of sedimentary rocks. Throughout northeastern Ohio, the Sharon Conglomerate is noted for the formation of massive cliff faces, rock shelters, and slump blocks (Rau, 1970). The designation "conglomerate" is somewhat misleading. Pebble size is extremely variable, ranging from about 1 mm to 5 cm, and occasionally even larger (Heimlich et al., 1970). There may be abrupt lateral gradation in pebble size, a feature strikingly evident on Little Mountain. Coogan et al. (1974) map two prominent belts of Sharon Conglomerate notable for large pebbles, one belt of which terminates at Little Mountain. About 90% of the pebbles are milky quartz, with limonite as the usual cement. Differential weathering of this cement results often in honeycomb patterns in the cliff faces (Heimlich et al., 1970).

At the base of the Sharon formation lies a major disconformity with the Meadville Shale of the Cuyahoga group of Mississippian age sediments. This disconformity is responsible for two phenomena which contribute to the habitat supporting the populations of *Vittaria*, namely, the origination of springs and the formation of slump blocks. The Sharon Conglomerate is highly permeable, whereas the underlying shale is relatively impervious. This disconformity, then, is marked by a zone of seeps and springs (Heimlich et al., 1970; Rau, 1970). The jointed conglomerate tends to slip along this lubricated shale surface, splitting the rock, which slowly moves downslope. On Little Mountain this joint-controlled slippage forms a picturesque and complex system of blocks and chasms ranging from 1 to 3 m wide, occasionally narrower, 10 to 15 m deep, and often as long as 50 m (Aronson, 1974).

The springs which flow from the disconformity on Little Mountain are exceptional in that they average 8–9°C year-round (Parsons, pers. comm.). This cold temperature allied with the depth and narrowness of the fissures on the mountain permits snow and ice to persist long into the warmer months. The writer noted the remains of ice on 10 June 1982. Even in mid-summer one's breath condenses before one's face while walking through the chasms on the mountainside. The environment within the crevasses of Little Mountain conforms in every particular to the ecological requirements of *Vittaria* as outlined by Farrar (1978, p. 4): "a low light intensity of 100 ft-c or less, relatively high humidity, and protection from temperature extremes . . . overhanging rock outcrops, dense forest canopy, and nearness to running water."

Floristically, Little Mountain is a part of the White Pine–Hemlock–Northern Hardwoods community (Braun, 1950), a forest association of very limited occurrence in Ohio. The first botanist to visit the mountain may have been John L. Riddell, who collected several species from this "pine-clad, rubblestone knob" (Riddell, 1836, p. 567). Read (1873a, b) listed the major forest trees of the mountain, particularly noting the Hemlock (*Tsuga canadensis* (L.) Carr.) and White Pine (*Pinus strobus* L.) on the northern end of the mountain, the extensive growth of American Chestnut (*Castanea dentata* (Marsh.) Borkh.) throughout the summit, and "Rock Oak" (*Quercus prinus* L.) on the southern knob. All these species are yet extant on the mountain, although the chestnut is represented only by fallen, dead trees and root sprouts. Ferris (1887) presented an extensive list of vascular species for the mountain. While his list contains some obvious inaccuracies, it also provides further evidence that most of the herbaceous and woody species found on Little Mountain in the past still grow there today and that the original vegetation conformed to Braun's concept of the White Pine–Hemlock–Northern Hardwoods community.

In most of its known range, the *Vittaria* gametophyte seems associated with the Mixed Mesophytic forest as defined by Braun (1950). This is the case, for instance, with other known Ohio populations. However, the Warren County, Pennsylvania station (Farrar et al., 1983), like Little Mountain, is within the White Pine–Hemlock–Northern Hardwoods floristic province. The occurrence of *Vittaria* gametophytes probably is more closely related to appropriate physical and geological setting than to floristic province.

Little Mountain was a prominent landmark to the first settlers of northeastern Ohio. As early as 1831, a hotel was built on the mountaintop, and within the following 50 years Little Mountain became a celebrated resort. At least three hotels were built on the summit, together with a complex of summer cottages, gazebos, churches, schoolhouses, and bowling alleys. The largest and best-known of the hotels, the Pinecrest, built in the late 1880's, featured a Western Union telegraph line and a post office. The cool springs also induced developers to advertise water cures for "invalids." Guests clambered through the chasms on sweltering summer days, enjoyed the cool breezes through the white pines, and gazed at the dramatic view of Lake Erie from the northern knob. It was fashionable to carve one's name on the conglomerate in the "Devil's Kitchen," as one large grotto was dubbed. Many of these graffiti are still legible today, a sort of permanent guest register. The resort era ended by 1920 and the Pinecrest hotel was torn down in 1941. Little Mountain ceased to be the playground of the public and instead became the private preserve of the Little Mountain Club, an elite group of wealthy Clevelanders (Ahlstrom, 1961; Ferris, 1887). The mountain could then recover from the years of wanton vandalism. The present composition of the vegetation and the beautiful stand of mature White Pine are tributes to the ability of plant communities to survive and recover from severe disturbance. Other than the graffiti on the rocks, now largely cloaked by bryophytes, the most notable evidence of the former resort is the abundance of *Vinca minor* L. on the mountaintop.

Little of the disturbance described above would have had a direct effect on the *Vittaria* population. However, it is difficult to be certain how common or widespread the gametophytes might have been prior to the time of the hotels. Today, the *Vittaria*, although occurring over a considerable linear area of the mountainside, grows in isolated pockets, often only a few square cm in extent, on the walls of the darkest and narrowest of the crevasses formed in the Sharon Conglomerate. The plants do not form great mats of vegetation covering entire rock faces as described by Farrar (1978) or as observed by the author in the Hocking Hills of southeastern Ohio. An occasional colony of the gametophytes occurs in the cast left by the fall of a particularly large quartz pebble. Most often the plants grow in recesses or narrow clefts formed in zones of finer pebble size. The plants definitely are less frequent in the areas of coarser pebbles.

Since this population of *Vittaria* gametophytes is the first reported from glaciated regions, it is interesting to speculate on the mode of introduction of the species to Little Mountain. In this regard, it must be clearly stated that Little Mountain was not a nunatak. Read (1873b) found granite boulders on the mountaintop and White (1980, 1982) maps thin layers of Hiram Till of Wisconsinan age over even the highest summits of the limits of the Appalachian Plateau in Ohio. Clearly, Little Mountain was not a refugium on which individuals of *Vittaria* could have survived glaciation.

The means of dispersal of this species, even in the heart of its range, is little understood. Although *Vittaria* gametophytes prolifically produce vegetative gemmae, there seems to be no obvious mechanical means for transporting these gemmae across the 90 km gap between Little Mountain and the nearest limit of the

Wisconsinan ice. It seems unlikely that the few-celled gemmae could survive wind-borne dispersal over such a distance without fatal desiccation. Also, it is difficult to understand how wind currents can lift these gemmae from the sheltered grottos and canyons in which they occur and convey them into the upper air. A possibility, which seems highly unlikely at least to this writer, is that the plants were introduced by an animal or human visitor who had accidentally picked up the gemmae in southeastern Ohio only a short time before.

Both Farrar and this writer have found *Vittaria* gametophytes at the limit of Wisconsinan glaciation in Fairfield County, Ohio, yet have failed to locate the species in similar habitats and on the same rock strata in areas only a few kilometers beyond the glacial boundary in other Ohio counties. Farrar's two western Pennsylvania stations for *Vittaria* gametophytes are located in Lawrence and Warren counties. The Lawrence County site is about 80 km southeast of Little Mountain and is located just north of the Illinoian glacial limit and south of the Wisconsinan boundary. The Warren County population is about 160 km east-northeast of Little Mountain and is directly south of the Illinoian limit. At present, the Warren County station is the northernmost known occurrence of these gametophytes (Farrar et al., 1983).

It is probably useless to speculate overmuch on the origin of the Little Mountain population of *Vittaria* until other, similar sites on the glaciated Appalachian Plateau of Ohio and nearby states are examined for this species. Appropriate habitats elsewhere in glaciated regions may well harbor populations of this gametophyte. Indeed, the perennial gametophyte of an as yet unknown species of *Trichomanes* has been found on the glaciated Appalachian Plateau from central Ohio to New Hampshire (Farrar et al., 1983; McAlpin et al., 1978). Perhaps this find of *Vittaria* should not come as such a surprise after all.

In glaciated Ohio, suitable habitats are very limited in extent and highly disturbed. If the case of Little Mountain is considered, however, disturbance which may have extirpated other types of vegetation may not have had so severe an effect on *Vittaria*. As of this writing, *Vittaria* gametophytes have not been found elsewhere in glaciated Ohio. But much field work remains to be done before any firm conclusions can be reached as to the true distribution of the gametophytes, either nationally or statewide. This find opens new realms for fern enthusiasts to explore.

The author is indebted to R. Henry Norweb, Jr., Director of the Holden Arboretum, for access to the Arboretum property and for permission to collect vouchers. Brian Parsons and Thomas Yates of the Arboretum staff have provided field assistance as well as access to unpublished data on Little Mountain and its history. The Arboretum and its staff should be congratulated for their commitment to the protection of natural areas. Mr. and Mrs. Hugh Pallister of Willoughby, Ohio, also have provided the author with information on the history of Little Mountain. My special thanks are owed to Dr. Donald R. Farrar of Iowa State University, Ames, Iowa, for verifying the identity of the *Vittaria* gametophytes, for his sharing of data, and for his encouragement. This research was supported by the Division of Natural Areas and Preserves, Ohio Department of Natural Resources.

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Chapman's Quillwort Reconsidered

BRIAN M. BOOM*

Certainly one of the least known pteridophytes in the southeastern United States is Chapman's Quillwort. Described by Engelmann (1882) as *Isoëtes flaccida* Shuttlew. var. *chapmanii* Engelm., the taxon has been collected only a few times since its initial collection by A. W. Chapman in 1848. The collections are always from the same general locality in Jackson County, Florida. Larger megaspores with smoother ornamentation were said by Engelmann to distinguish it from the typical variety.

Underwood (1900) and Clute (1928) both recognized the distinctness of the taxon, and Small (1932) even elevated it to specific status. Lakela and Long (1976) maintained *I. chapmanii* (Engelm.) Small, and in their key distinguished it from *I. flaccida* on the basis of megaspore ornamentation and sporangium shape. On the other hand, Pfeiffer (1922) and Boom (1979, 1982) were not convinced of the distinctness of *I. chapmanii,* and they synonymized it with *I. flaccida*. Recently I was able to study the spores of these plants more carefully by means of scanning electron microscopy (SEM), and I now regard the evidence as sufficient for maintaining *I. flaccida* var. *chapmanii* as a rare, but distinct element of Florida's pteridophyte flora.

Spores were coated by a two-step procedure consisting of the deposition from a low voltage arc of an initial carbon layer onto which was subsequently sputtered a 60:40 gold-palladium alloy using a 15 watt DC diode coater. Specimens were examined with a Cambridge S4-10 SEM. Photographs were taken with Polaroid Type 665 Positive/Negative Land Film. Spores of some thirty specimens of *Isoëtes flaccida* were examined (vouchers cited in Boom, 1979), but the photomicrographs of only three are presented herein: var. *flaccida:* Lake Flirt, near Lake Okeechobee, Florida, Aug 1878, *A. P. Garber s. n.* (US 240797); cypress pond near Cobb, Sumter Co., Georgia, *R. M. Harper 1046* (US 400120); and var. *chapmanii:* Tributary of the Chipola River at Marianna, Jackson Co., Florida, *R. K. Godfrey 61963* (US 2424571).

Both megaspores and microspores of the two varieties show differences in perine ornamentation which are taxonomically significant (*Figs. 1–6*). Additionally, the differences in megaspore size provide a useful means of distinguishing the varieties.

The ornamentation of *I. flaccida* var. *chapmanii* megaspores is low tuberculate, densely so on the distal hemisphere and sparsely so on the proximal (*Fig. 1*). Greater magnification shows the perine to be minutely echinate (*Fig. 3*). In var. *flaccida,* the megaspores are also low tuberculate, but densely so on both hemispheres (*Fig. 2*). Greater magnification reveals a finely rugulate perine, the muri anastomosing so as to give a spongy appearance (*Fig. 4*). The diagnostic perine characters (extent and distribution of tubercules) can be seen at 40X, and the size difference detected with a dissecting microscope.

Although the microspores of the varieties are essentially the same size, their perine ornamentation differs: that of var. *chapmanii* being echinate with an arach-

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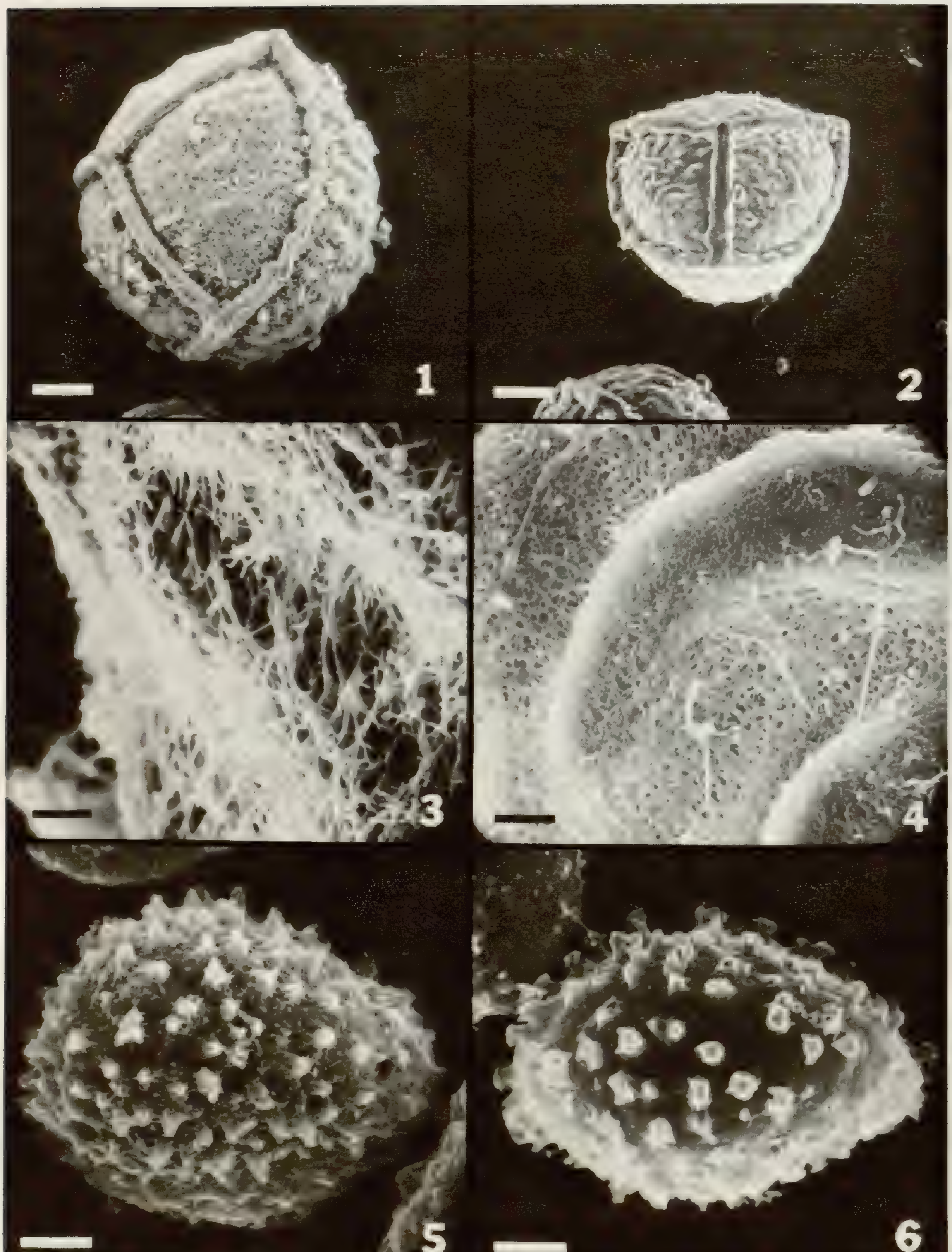

FIGS. 1–6. *Isoëtes flaccida* spores. FIG. 1. Megaspore of var. *chapmanii* (US 2424571); scale = 100 μm. FIG. 2. Megaspore of var. *flaccida* (US 240797); scale = 100 μm. FIG. 3. Megaspore perine of var. *chapmanii* (US 2424571); scale = 7 μm. FIG. 4. Megaspore perine of var. *flaccida* (US 240797); scale = 7 μm. FIG. 5. Microspore of var. *chapmanii* (US 2424571); scale = 5 μm. FIG. 6. Microspore of var. *flaccida* (US 400120); scale = 5 μm.

noid perine between echinae (*Fig. 5*), and that of var. *flaccida* being papillate with a laevigate perine between papillae (*Fig. 6*). Given their average size of ca. 30 μm, the microspores do not provide useful taxonomic characters for the field or herbarium botanist, but the ornamentation differences help confirm their distinctness.

Aside from the spore characters, there are no other apparent morphological, chemical, or ecological differences that separate the varieties. The orbicular or obovoid sporangium ascribed to var. *chapmanii* by some authors (Engelmann, 1882; Small, 1932; Lakela & Long, 1976) as a feature distinguishing it from var. *flaccida* (with an oval, ellipsoid, or subglobose sporangium) is not a good character, as this structure varies too much depending on plant size and ecological conditions. The flavonoid chemistry of the two varieties was examined by Boom (1979), but the chromatographic profiles were identical. Ecologically, there appears to be nothing striking about the habitat of var. *chapmanii*. A topotype collection (*Boom 333*, TENN) reports "sandy/peaty substrate, clear water in deep bald cypress swamp;" the stream is underlain by limestone. This general description could apply to many areas in Florida where var. *flaccida* occurs, but perhaps there are significant microhabitat factors involved which have not yet been detected. A distribution map of *I. flaccida* is given in Boom (1982).

Just as Taylor et al. (1975) used SEM to confirm the distinctness of *Isoëtes butleri* Engelm. from *I. melanopoda* Gay & Dur. based on spore ornamentation, it has been possible to show that two entities are encompassed by *I. flaccida*. I prefer to recognize these two taxa at the varietal level because, unlike the case of *I. butleri* and *I. melanopoda*, the two taxa involved here are not ecologically or geographically differentiated. I do not regard *I. flaccida* var. *chapmanii* as a hybrid because it meets none of the criteria used in the detection of several instances of hybridization in other southeastern U.S. quillworts (Boom, 1982). I consider *I. flaccida* var. *flaccida* to encompass *I. alata* Small and *I. flaccida* var. *rigida* Engelm. The following key separates the two recognized varieties of the species:

KEY TO VARIETIES OF ISOËTES FLACCIDA

Megaspores 300–400(440) μm diam., densely low tuberculate on both hemispheres; microspores papillate; common throughout Florida and southern Georgia ..... var. *flaccida*

Megaspores 440–540 μm diam., densely low tuberculate on distal hemisphere, sparingly so on proximal; microspores echinate; rare in northwestern Florida (Jackson Co.) ..... var. *chapmanii*

Appreciation is extended to David Lellinger, Andrea Sessions, and Walter Brown for assistance with *Isoëtes* spore studies at US. The present work was materially aided by the Botany Department of The University of Tennessee, Knoxville, by a Grant-In-Aid of Research from Sigma Xi, and by a travel grant from The Smithsonian Institution.

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REVIEW

Flora Malesiana, Series II–Pteridophyta, volume 2, part 5, Thelypteridaceae, by R. E. Holttum. Pp. 331–599, including index and addenda for entire volume, plus pp. 1–20, contents and dedication. 1982. Martinus Nijhoff, BV, The Hague, Netherlands. $63.00.—Historically, no other group of ferns has been subjected to such varied circumscriptions, both of the family and genera; moreover, species have been notoriously under-collected, ill-defined and confused, and their relationships misunderstood. Part of the reason is their mundane (cringe) and superficially similar look that causes collectors to sample one or a few and pass by the rest. Another reason is that few taxonomists have bothered to look at them closely. The first who did look was Carl Christensen, to whom Holttum appropriately dedicates this volume; but Christensen concerned himself mostly with Neotropical species. In 1963, Ching presented a revised classification of Old World genera that provided a springboard for Holttum's many precursory revisions culminating in the present work.

The sheer size and complexity of Thelypteridaceae have made Holttum's task formidable. This family is probably the largest in ferns, with almost 1000 species. In the Flora Malesiana region alone Holttum treats 440 species in 22 genera. The number of new taxa (75 species, 18 varieties) is staggering and reminds us how poorly known are the tropical floras and how urgent it is to preserve what little is left. In *Sphaerostephanos*, with 152 Malesian species, 43 are known only from the type and many additional species are not much better represented in herbaria.

But Holttum's most important contribution is not the number of species named and redefined; it is the understanding of the large natural groups of species. Here, he has brought order from chaos. Doubtless there will be taxonomists, including myself, who will prefer to assign lower rank to some of Holttum's genera. But his circumscriptions of natural groups are likely to survive intact or with only minor redefinition.

At least 13 new chromosome counts are embedded in the work; they may well be overlooked by compilers of chromosome indices. The most interesting, $n=66$ for a species of *Coryphopteris*, is a new base number ($x=33$) for Thelypteridaceae and may lend support to Holttum's contention of a relationship between this family and Cyatheaceae.

The magnitude, originality, and scholarship shown in this work are truly impressive and culminate a brilliant career. But Holttum is already turning to other ambitious projects and one wishes him many more years of taxonomic insight. *—Alan R. Smith, Herbarium, Department of Botany, University of California, Berkeley, CA 94720.*

C-Glycosylxanthones in Diploid and Tissue Culture-induced Autotetraploid Davallia fejeensis

P. MICK RICHARDSON and HARINDER K. PALTA*

1,3,6,7-tetrahydroxy-*C*-glycosylxanthones are phenolic compounds which have been found relatively infrequently in ferns. A recent survey (Wallace et al., 1982) reported their occurrence in seven genera: *Asplenium*, *Athyrium*, *Elaphoglossum*, *Cardiomanes*, *Hymenophyllum*, *Trichomanes*, and *Marsilea*. They have also been reported in *Ctenitis decomposita* (Bohm, 1975). The present communication reports *C*-glycosylxanthones in *Davallia fejeensis* Hooker. Diploid and tetraploid samples of both the sporophytic and gametophytic generations were examined.

MATERIALS AND METHODS

Rhizome tips (about 2 cm long) of diploid *Davallia fejeensis* were collected in the Enid A. Haupt Conservatory of the New York Botanical Garden, cleaned, rinsed in tap water and further trimmed. Voucher specimens are at NY. Explants (6-8 mm long) were cultured on 1% agar-gelled sterile nutrient medium of Knudson as modified by Steeves et al. (1955) and supplemented with 2% sucrose in order to provide control diploid sporophytes growing in axenic culture. Roots, leaves, and rhizomes of the resulting plants were excised and induced to differentiate into aposporous diploid gametophytes. Stock cultures of diploid gametophytes were multiplied and further grown on liquid media supplemented with 0.6% agar to effect fertilization and raise tetraploid sporophytes. Tetraploid gametophytes were isolated from this tissue culture-induced tetraploid material by repeating the procedure followed at the diploid level. In this way, both diploid and tetraploid sporophytes and gametophytes were made available for this study.

Phenolic compounds were isolated by two-dimensional paper chromatography of an 80% methanol extract of green material in t-BuOH–HOAc–H_2O, 3:1:1 (TBA) and 15% aqueous acetic acid (HOAc), followed by one-dimensional paper chromatography in water. *C*-glycosylxanthones appeared as orange compounds in ultraviolet light and turned yellow when fumed with ammonia. Both purified compounds were co-chromatographed with mangiferin and isomangiferin isolated from *Asplenium montanum* Willd. *(Bozeman & Radford 11552*, NY). R_f values in TBA, BAW, HOAc, and H_2O were: mangiferin, 0.31, 0.43, 0.43, 0.12; isomangiferin, 0.19, 0.29, 0.23, 0.04; *Asplenium* mangiferin, 0.34, 0.42, 0.42, 0.11; *Asplenium* isomangiferin, 0.21, 0.32, 0.23, 0.03; and rutin standard, 0.43, 0.45, 0.56, 0.25. The BAW and HOAc values are very similar to those of Smith and Harborne (1971), but the TBA and HOAc values differ from those of Markham and Wallace (1980). Absorption spectra (MeOH, nm) were: mangiferin, 232, 260, 270sh, 310, 364; isomangiferin, 240, 258, 270sh, 312, 365. The compounds were unaffected by acid hydrolysis (1 hr, 2N HCl, 100°C).

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RESULTS AND DISCUSSION

The *C*-glycosylxanthones mangiferin and isomangiferin were the only phenolic compounds appearing on the two-dimensional chromatograms of an 80% methanol extract of each sample. The diploid and tetraploid sporophytes contained relatively large amounts of both compounds, but in both cases the mangiferin spot was much larger than the isomangiferin spot. Gametophyte extracts contained very small amounts of each compound. Further identification was performed only on compounds from the sporophytes. Spots from the chromatograms were eluted and then chromatographed in water to purify them sufficiently for ultraviolet spectrophotometry and co-chromatographic testing. The purified compounds showed reduced R_f values in comparison to those measured on the two-dimensional chromatograms, strongly suggesting that R_f values based on such chromatograms may be misleading.

These results suggest that the same *C*-glycosylxanthones are produced in both sporophytes and gametophytes. This is comparable to the only similar published study of fern flavonoids (Petersen & Fairbrothers, 1980), where the same flavonol glycosides appeared in both generations. Secondly, it appears that an induced doubling of the chromosome number in *Davallia* has no effect on the production of *C*-glycosylxanthones in either generation. If we accept that the *C*-glycosylxanthones in *Davallia* are equivalent to the flavonoids in flowering plants, then the effects of induced chromosome doubling on phenolic production in ferns may be compared with the effect of a similar chromosome doubling in angiosperms. Mears (1980) has reviewed the chemistry of polyploids. In some cases of induced autotetraploids in *Phlox* (Levin, 1968), no qualitative differences in phenolics were detected; in another study in the same genus (Levy, 1976), such differences did occur. In *Briza* (Murray & Williams, 1976) qualitative differences in phenolic production sometimes occurred in induced tetraploids. A more complex situation occurred in autotetraploids of *Gibasis* (del Pero de Martinez & Swain, 1977), where polyploidy is correlated with Robertsonian Fusion, a phenomenon which may be responsible for changes in phenolic expression.

This is the first study of the chemistry of induced autoploidy in fern gametophytes and sporophytes. The tissue culture method followed in this study is an excellent way to effect such changes in chromosome numbers. A survey for the presence of *C*-glycosylxanthones in other fern genera is being undertaken in our laboratory; it is possible that these compounds may not be as rare as they were previously thought to be.

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REVIEW

THE GENUS SELAGINELLA IN TROPICAL SOUTH AMERICA, by A. H. G. Alston, A. C. Jermy, and J. M. Rankin. Bull. Brit. Mus. (Nat. Hist.), bot. ser. 9(4):233–330. 1981. £14.00 postpaid.—A. H. G. Alston was the premier *Selaginella* authority in the middle of this century. He published extensively on the genus in the Old World and in southern South America, Brazil, the West Indies, and Central America in the New World. At the time of his death, he had begun to study *Selaginella* from the Andean countries and the Guyanas. The present paper completes and extends Alston's work and includes Brazil, thus accounting for virtually all of tropical South America. The region contains 133 species and six infraspecific taxa of *Selaginella*. A table of species distribution by countries shows that Colombia has by far the greatest number of species. The bracketed key to the species can be read forward or backward, a decided advantage because there are no species descriptions. Each taxon treated has a synonymy, a statement of range, a list of specimens, and, sometimes, additional notes. The authors have uncovered some overlooked synonyms in rare literature, always a pleasure to see. However, most synonyms state only the country where the type was collected, rather than the type locality, the collector and number, and the herbarium of deposit. A list of references and an index to accepted names and synonyms concludes the volume. New taxa are illustrated by a photograph of the herbarium sheet and by SEM photographs of the leaves, which range in magnification upwards from a mere eight times natural size, a useful technique for illustrating clearly the cilia and other small details of the leaves. This paper is indispensible for identifying Selaginellas from tropical America and will be the standard reference for many years to come.—*D.B.L.*

The Distribution of Woodwardia areolata

R. CRANFILL*

Phytogeographical studies in North America, as compared with those in Europe, are still in their infancy. Lack of detailed atlases and the relative paucity of extensive paleo- and neoecological studies in North America hamper the botanist who wishes to investigate the factors affecting the distribution of a particular species. A few botanical studies of this sort are available (Hocker, 1956; Koevenig, 1976; Salisbury, 1926), although most are limited to local areas or to single factors.

The distribution of a particular plant is determined by several interrelated factors, including: (1) climate and soils, both present and past, (2) interactions with other organisms, (3) production and dissemination of propagules, and (4) evolutionary history, including time and place of origin (Billings, 1952; Cox et al., 1976; Krebs, 1972; Pielou, 1979). In general, physical parameters of the environment, such as moisture availability or extremes of temperature, place absolute limits on the distribution of an organism. Interactions with other species (including man!), soils, dispersability, and other historical factors (e.g., hurricanes, stream piracy, and glaciation) constrain the organism within these bounds (Billings, 1952; Gorham, 1954). As many have pointed out (Cox et al., 1976; Koevenig, 1976), the study of the interaction of limiting factors is problematic because of our inability to deal quantitatively with several seemingly inextricably linked variables at once. Analysis of widespread or narrowly restricted species is often easiest because in these situations one or a small number of variables contributes differentially to the distribution. Even so, the implications of such correlations are not always as clear as they may seem. In the absence of corroborative experimental evidence, caution should always be exercised in the interpretation of distributional correlations.

Woodwardia areolata (L.) Moore is ideal for this type of study because it is widespread and common throughout the southeastern and Atlantic United States and is well collected. One of the three species in subgenus *Lorinseria*, it is characteristic of acidic mucky, sandy, and peaty bogs throughout the southeastern United States (Wherry, 1921, 1964). The aim of this paper is to make some ecological inferences from the distribution of *W. areolata* and to discuss some of the problems inherent in this sort of induction.

MATERIALS AND METHODS

The distribution of *W. areolata* was compiled from herbarium specimens deposited at the following institutions: DHL, F, FLAS, FSU, GH, KY, MEM, MICH, MO, NCU, NY, SMU, TAES, TENN, TEX, TNS, UC, USF, VDB (abbreviations of Holmgren et al., 1981). Over 700 sheets were examined and plotted accurately on a base map of the eastern United States and Canada. Climatic and edaphic parameters were drawn from a variety of sources. Isotherms were composed and redrawn from individual state maps (National Atmospheric and Oceanographic Institute, 1980).

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RESULTS AND DISCUSSION

The distribution of *W. areolata* is shown in *Fig. 1*. A specimen found at USF (*Cheever s. n.*, 25 June 1917) verifies the occurrence of this species in Maine (previously questioned by Ogden et al., 1948). It also seems likely that the species may occur in southern Indiana and extreme eastern Kansas. Associations of the distribution with several edaphic and climatic factors were found and are discussed below.

Climatic Factors.—The climatic feature that appears to have the greatest influence on *W. areolata* is minimum winter temperature. Of the three isotherms examined (0°C, −2.0°C, and −4.5°C), the −4.5°C mean made the closest fit. All stations, save five, fell to the south of the line, with especially close correspondence in New England. Of the sites north of the isotherm, three are no longer extant (Kitfield, 1974; Price, pers. comm.), while another lies close to the Atlantic Ocean which may have a moderating influence not reflected in the climatic data. It is interesting to note the absence of this species from the higher Appalachians of Virginia and West Virginia (Wagner, 1963), even though suitable acidic bogs and seeps exist in the area.

It is apparent that mean temperature in itself is not a very useful index. As an indicator of potential climatic severity it can be important, although analysis is nearly impossible in the absence of values for variance. Thus, survival of *W. areolata* may not depend as much on its tolerance of −4.5°C as on its ability to withstand the occasional much colder winter. Of course the problem may be even more complex. Winter minima may reflect other associated parameters, such as the length of the growing season, that more directly affect the ability of the plant to grow, reproduce, and compete with its neighbors.

Competition can be critical in the distribution of organisms (Hynes, 1954; Jaeger, 1970). Since competition varies as a function of community composition, which changes over the distribution of any particular species, a perfect or even very close fit between abiotic influences and distributional limits often does not obtain. Distributions of weedy species, therefore, probably more closely parallel absolute climatic limits than do distributions of plants of stable habitats, where interactions with other organisms are more structured. The recent northward spread of *Asplenium platyneuron* (L.) B.S.P., primarily a southern species, is a result of an increase in the disturbed habitats that provide this species with suitable sites in which to become established (Wagner and Johnson, 1981) and demonstrates that the previous exclusion of this spleenwort was more a result of its competition with established communities than a result of its tenderness. A similar explanation may account for the presence of *W. areolata* on siliceous cliffs and ledges at the northern and western limits of its range, even though seemingly suitable bogs and seeps exist in these areas. At some point, the species composition of the typical habitat of this species changes sufficiently so that it no longer is competitive in such situations. Sandstone cliffs and ledges in the same vicinity, which present physiological demands similar to those of acidic bogs (in the form of nutrient inavailability and drought stress), possess less plant cover and are characterized by a much lower diversity of species. It seems likely, therefore, that lithophily in *W. areolata* may be a

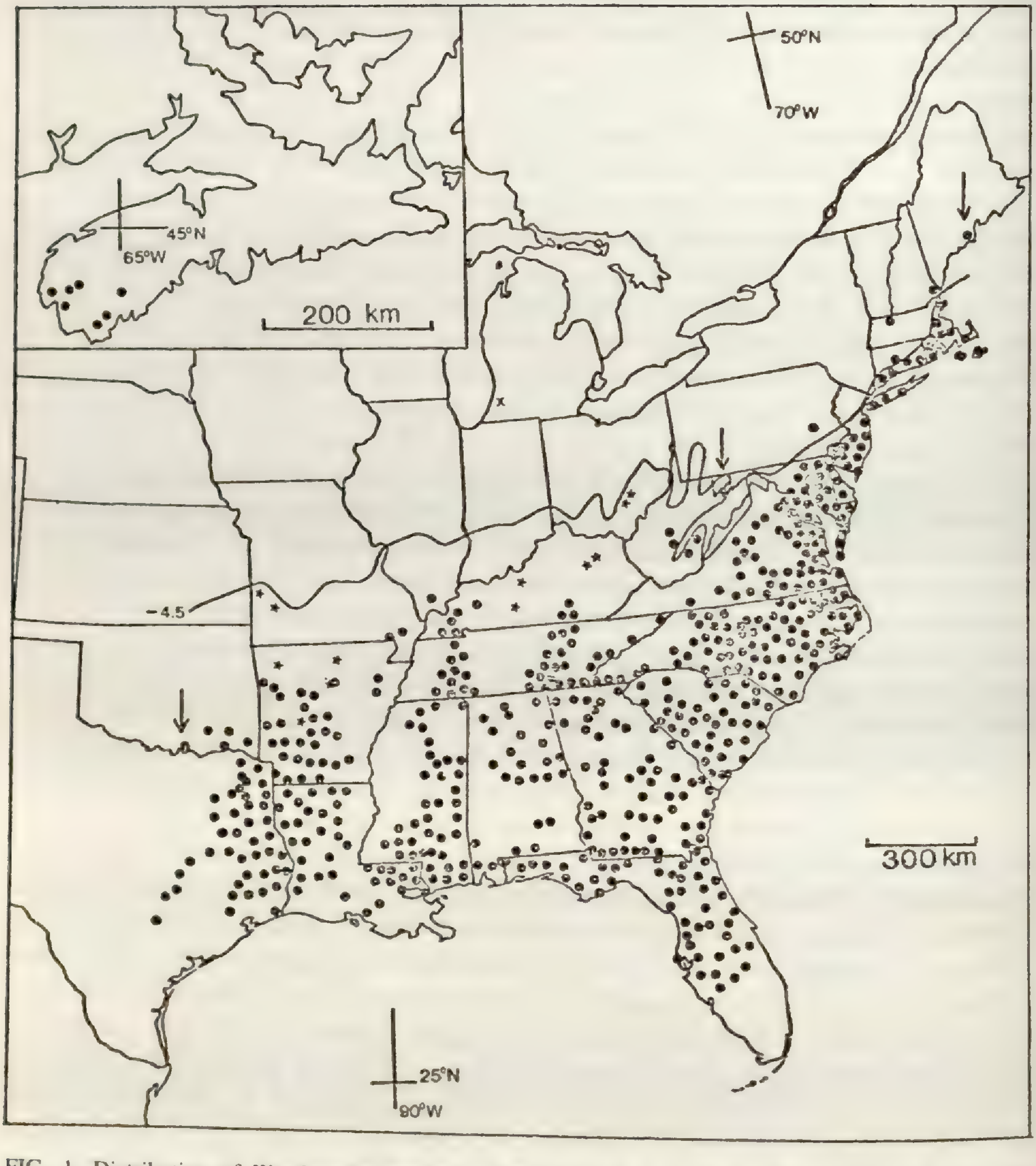

FIG. 1. Distribution of *Woodwardia areolata*. Dots represent terrestrial and unspecified occurrences while stars indicate epipetric stations. The ragged line represents the January −4.5°C isotherm. Inset shows Canadian province of Nova Scotia. X indicates extirpated population. Arrows indicate outlying populations.

direct response to competition. Such cases would be parallel to but more subtle than Billings' (1950, 1952) "Compensation Effect," in which edaphic factors of certain soils and rock types compensated for the negative effects of other environmental factors. Transplants of individuals of *W. areolata* from Kentucky to Michigan survived over two winters (until 1981 when the experiment was discontinued) and indicate that winter minima alone are insufficient to account for the distribution of this fern. Further demographic and transplant experiments are needed to adequately test the hypothesis that competition is the controlling factor.

Edaphic Factors.—The distribution of *W. areolata* fitted that of certain soil types even better than it did temperature. My measurements and those of Wherry (1921) indicate that the sporophyte of this fern is extremely acidophilous. The pH of several sites checked in Kentucky and Tennessee all fell below 5.5, with one reading of 4.0. It is not surprising then that the species is entirely absent from calcareous regions within its range. No stations are known in the limestone regions of the Interior Low Plateaus or in the calcareous Black Belt region of Alabama and Mississippi. Absence of the species from glaciated areas in southern Illinois and southeastern Ohio can be ascribed to the predominance of calcareous glacial drift in these areas *(Fig. 2)*. The alluvial plain of the lower Mississippi River is also avoided. As a region of heavy basic to circumneutral clays (Kellogg, 1936; Braun, 1950), the Mississippi Alluvial Plain is devoid of most species characteristic of the sandy uplands and acidic seeps to the east and west. Correspondence of the distributions of *W. areolata* and *Pinus echinata* Miller (Little, 1971), another calcifuge, is striking.

The best fit to soils occurs in eastern Texas (see inset, *Fig. 2*). The absence of the Chain Fern from the regions of the Blackland Prairie and Coast Prairie soils, both predominantly calcareous clays (Arbingast et al., 1976), is striking. Because of their greater matrix potential, clay soils must be hydrated to a higher percentage than coarser grained soils to exceed the permanent wilting percentage. As a result, clay soils tend to be droughtier in more arid regions and may become critical for *W. areolata* as it reaches its western limit. The patchwork distribution of these soils has made it impossible, therefore, to assess the relative importance of moisture availability (for an index, see Thornthwaite, 1948) and relative humidity as limiting factors; no good correlation was found between these factors and the western limit of *W. areolata*.

As with the consideration of climate, distributional evidence is insufficient to demonstrate that heavy clay soils or pH are in themselves limiting. The indefinite survival of adult sporophytes on the heavy, calcareous, nutrient-rich soils of the Inner Bluegrass region of Kentucky indicates that competition may actually constitute the limiting factor.

The absence of this fern from much of the Allegheny Plateau cannot be explained by the climatic or edaphic criteria just discussed. Contrary to its name, the plateau region is highly dissected and affords little of the seep and bog habitat necessary for the species. It also lacks extensive deposits of resistant sandstone and conglomerate that form the secondary habitat of the fern.

Although the previous discussion concerned the sporophyte, other stages in the life history may be important in controlling the distribution. Pteridophytes are like

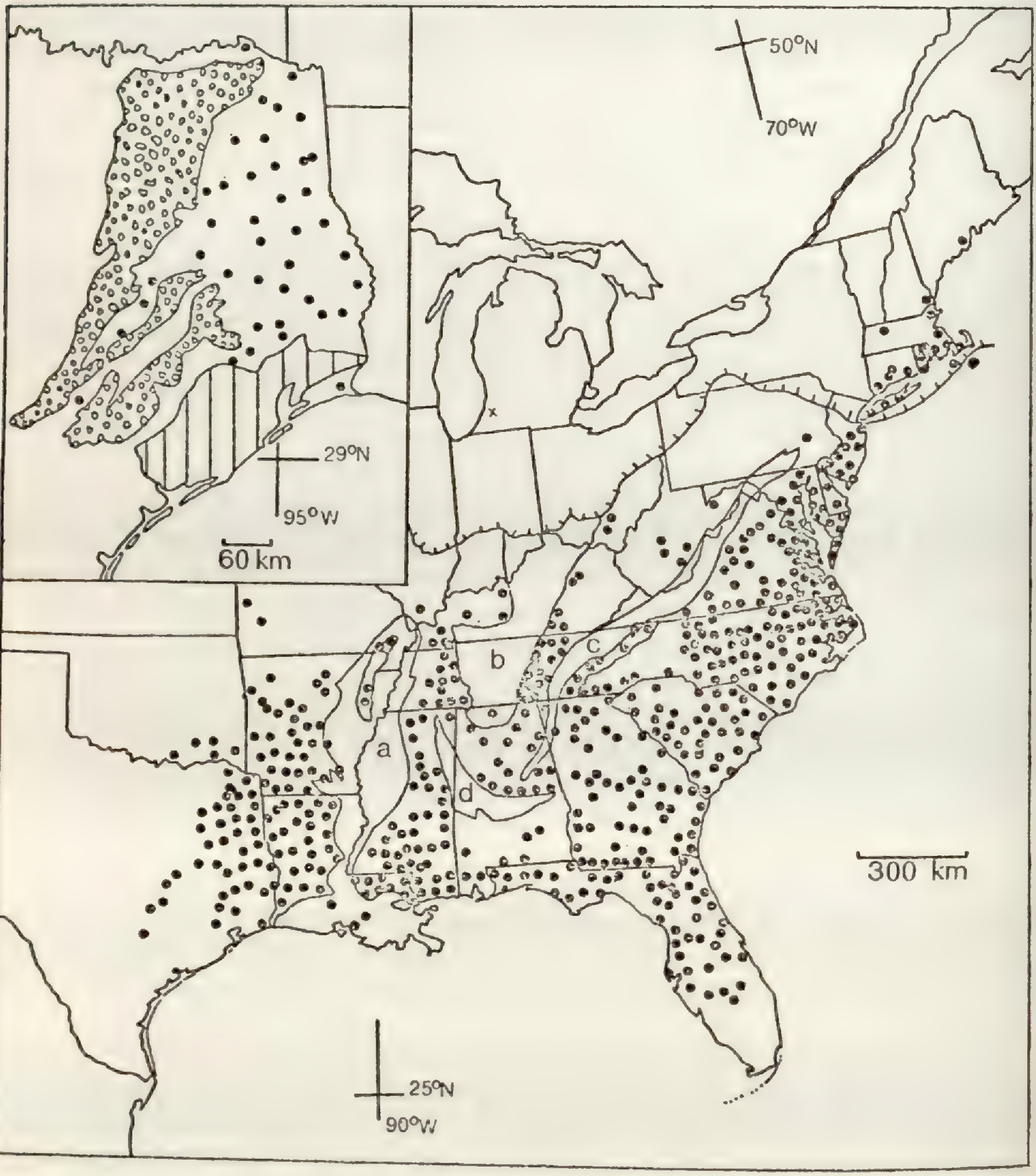

FIG. 2. Distribution of *Woodwardia areolata* in relation to soils; a = Mississippi Alluvial Plain, b = region of Interior Low Plateaus with calcareous soils, c = Ridge and Valley Province, d = Black Belt region. Inset shows enlargement of the distribution in Texas; cobbled area represents the region of blackland prairie soils while crosshatched area represents the extent of coastal prairie soils. Hatched line depicts extent of Wisconsin Glaciation. X indicates extirpated population.

lower plants in which the alternation of generations can have drastic consequences on the distribution of the organism (see the example of *Laminaria*, Dixon, 1965, pp. 109–115).

In summary, the present distribution of *W. areolata* is clearly associated with the mean −4.5°C minimum January temperature to the north. The distribution of calcareous soils, especially clays, effectively limits the distribution to the south and may be important, in concert with increasing aridity, to the west. No correlation was found between the distribution of this fern and the indices of moisture availability and relative humidity. In all cases it appears likely that competition narrows the limits imposed by abiotic influences since preliminary experiments demonstrate the ability of this species to survive in more rigorous environments when competition is removed. The change from bogs and seeps to cliffs and ledges at the range limit is also compatible with this hypothesis. This "competitional compensation point" is probably more important in limiting the distributions of non-weedy species, which occupy more stable habitats than do weedy species.

Experimental studies of problems of distribution are greatly needed. Through narrowing and refining our investigations, they may aid materially in the study of the effects of competition on community structure. Ferns make excellent subjects because they are small and fairly easy to grow and because the production and dissemination of propagules, critical in many flowering plants, is not so limiting in pteridophytes.

I am grateful to A. R. Smith and Herbert Baker who provided comments on a draft of this paper. I am indebted to D. L. Melroy who provided assistance and criticism in numerous ways.

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REVIEW

FERNS AND FERN ALLIES OF THE DRIFTLESS AREA OF ILLINOIS, IOWA, MINNESOTA AND WISCONSIN, by James H. Peck. Milwaukee Public Museum Contributions in Biology and Geology 53:1–140. 1982. $13.50 postpaid. —The driftless area, a pocket in the upper midwestern landscape which escaped at least the more recent glaciations, holds, by virtue of its topography and age of its habitats, a diverse and interesting array of plants. It has been the subject of botanical study for many years. The present account is by far the most complete and useful of any we have had for the pteridophytes, which number 73 species, 13 hybrids, and 6 infraspecific taxa. Peck's treatment includes a useful introduction, a discussion of the affinities of the flora with special reference to the interesting disjunct *Thelypteris simulata*, a systematic list with synonyms, statement of habitat, and specimen citations, a key to the genera and species of pteridophytes found in the driftless area, and a large and useful section of literature cited. Ninety. pages are devoted to full-page county distribution maps for the driftless area ferns that include all of Minnesota, Wisconsin, Iowa, Illinois, and Missouri. The maps not only place the ferns of the driftless area in the context of the surrounding region, but they are sure to stimulate searches for pteridophytes in counties where the first records are yet to be obtained.—*D.B.L.*

Two Moonworts of the Rocky Mountains; Botrychium hesperium and a New Species Formerly Confused with It

W. H. WAGNER, JR. and FLORENCE S. WAGNER*

The taxonomy of western North American botrychiums still needs much research. Interpretations of the past were based largely upon scanty and poorly prepared collections. For over 30 years only two *B. matricariifolium*-like moonworts have usually been accepted for this region—*B. boreale* subsp. *obtusilobum* (Rupr.) Clausen and *B. matricariifolium* subsp. *hesperium* Maxon and Clausen (Clausen, 1938). As to the former, we conclude that the western North American plant is not closely related to *B. boreale*, as will be discussed in a monograph of this genus currently in preparation. The correct name for taxon *obtusilobum* is *B. pinnatum* St. John (*Fig. 1*, a–g). Taxon *hesperium* also proves to be a distinct species, readily distinguished from *B. matricariifolium* A. Br. subsp. *matricariifolium*, which occurs in North America only east of the Great Plains (*Fig. 2*, h–n). With our recent opportunity to investigate large populations of these plants in the field in numerous localities, we are now confident of the distinctness of not only *B. pinnatum* and *B. hesperium*, but of a third element as well, which is described here for the first time.

It is no surprise to discover a new species related to *B. hesperium* in western North America, where the rate of endemism among moonworts is the highest in the world. With some ten out of 14 of the described and undescribed species known only there, western North America is clearly the metropolis for this subgenus (*Botrychium* subg. *Botrychium*). Using primarily the sterile lamina as a basis, we provide the following key to its major groups.

KEY TO THE GROUPS OF BOTRYCHIUM SUBG. BOTRYCHIUM IN NORTH AMERICA

1. Sterile lamina absent; frond composed of two sporophores.....*B. paradoxum* group
1. Sterile lamina present; frond with a single sporophore.
   2. Larger pinnae mostly fan-shaped or wedge-shaped, not pinnatifid; costa absent or poorly developed.
      3. Pinnae and lobes, especially the distal ones, commonly irregularly confluent; basal pinnae often strongly exaggerated.....*B. simplex* group
      3. Pinnae and lobes regularly separated; basal pinnae conform or only slightly exaggerated. *B. lunaria* group
   2. Larger pinnae mostly oblong to lanceolate, pinnatifid; costa usually present, at least in basal half of pinna.....*B. lanceolatum* group

Early in our studies we did not notice that the original collections of *B. hesperium* were mixtures of two species. Although certain specimens were different in a number of respects, we simply believed that some specimens had narrow, pointed segments and resembled *B. lanceolatum* and others had rounded segments and resembled *B. simplex*. We therefore assumed that *B. hesperium* was of hybrid origin,

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FIG. 1. Silhouettes of moonworts similar to *B. echo* and *B. hesperium*. FIGS. a–g. *B. pinnatum* (*Wagner 81113*, MICH). FIGS. h–n. *B. matricariifolium* (h, j, n, *Wagner 81003*, MICH; others *Wagner 81028*, MICH).

and that its apparent variability resulted from this. Our field studies, however, soon dispelled this interpretation. The type specimen of *B. hesperium* includes only individuals with rounded segments. It was taken at Glacier Lake in Rocky Mountain National Park by a high school teacher, E. Bethel, in 1914. Bethel and others took numerous specimens there during the period 1911 to 1921. Bethel was aware that there were actually two elements involved, and he and Ira Clokey separated their 1921 collection at Glacier Lake into two groups—*Bethel & Clokey 3987*, typical, and *3987a*, with "segments narrow, more acute." W. R. Maxon was also aware of these distinctive plants as shown by his annotations of one of the herbarium sheets (US984959).

Our new interpretation is based upon over 200 specimens of *B. hesperium* studied in the field in seven localities, and over 300 of the new species, *B. echo*, in ten localities. The two species grow in such similar habitats that one description of the habitat will suffice for both. They tend to occur together, often side-by-side. Also associated in genus communities with them in the southern Rockies are *B. lanceolatum*, *B. lunaria*, and *B. minganense*. In Montana and Alberta, where *B. echo* is not known, *B. hesperium* occurs also with *B. paradoxum* and *B. pinnatum*. Most of the localities that we studied had only a few plants. To illustrate, for *B. echo*, ten localities yielded respectively 1, 2, 2, 2, 3, 9, 11, 25, 97, and 150+ plants. The two most productive localities were in Arizona at Mount Baldy and at San Francisco Peaks. In the former locality, *B. hesperium* was absent, but at the latter we recorded 88 individuals of this species. At only one locality in the southern Rockies did we find only *B. hesperium* (*Wagner 81158*, 3 individuals in company with *B. lanceolatum*), but in the northern Rockies it apparently regularly occurs alone.

The two species grow on grassy slopes, roadsides, and at edges of lakes. The soil is usually rocky, the substrate including decomposed granite as well as other rock types. In the southern Rockies the plants grow at elevations between 8,500 and 11,500 ft. The easiest way to find them is to drive along roads at proper altitudes and to seek flat roadside ditches with gravelly soil and scattered shrubby vegetation, *Picea* saplings and *Salix* shrubs dominating. Plants are sometimes found growing even in the gravel of the road shoulder! In addition to spruces and willows, other woody associates encountered are *Lonicera involucrata*, *Potentilla fruticosa*, and species of *Abies*, *Juniperus*, and *Ribes*. The herbaceous associates include weeds and involve such genera as *Achillaea*, *Antennaria*, *Arenaria*, *Carex*, *Cerastium*, *Epilobium*, *Festuca*, *Fragaria*, *Frasera*, *Mertensia*, *Penstemon*, *Potentilla*, *Saxifraga*, *Sedum*, *Selaginella*, *Setaria*, *Solidago*, *Trifolium*, *Valeriana*, and *Zygadenus*. Seekers of these plants should be warned that only one out of ten or twenty seemingly appropriate habitats yield these botrychiums. It is therefore necessary to sample many likely sites.

Rather than distinguish only *B. hesperium* and *B. echo*, all of the North American taxa of the *B. lanceolatum* group that might be confused with them are keyed. For more details of the differences between *B. hesperium* and *B. echo* themselves, the reader is referred to the descriptions and to *Figure 4*. This key is based upon medium and large individuals.

FIG. 2. Silhouettes of moonworts. FIGS. a–i. *B. echo (Wagner 82107b,* MICH). FIG. j. A much divided form of *B. echo* (*Bethel & Clokey 3987a,* US; see also *Fig.* 3, a–e). FIGS. k–o. *B. hesperium* (k–n, *Wagner 82107a,* MICH; o, *Bethel* in 1914, US—type).

KEY TO THE BOTRYCHIUM LANCEOLATUM GROUP IN NORTH AMERICA

1. Sterile lamina broadly deltate, sessile to subsessile; sporophores of full-sized plants usually composed of several major upright axes; plants of northern North America.....*B. lanceolatum*
1. Sterile lamina mostly oblong to oblong-deltate, subsessile to stalked; sporophores of full-sized plants usually with one major upright axis, sometimes with one or two upright laterals.
   2. Sterile segment mostly conspicuously stalked, the stalk 20–30% of the blade length; segment tips usually serrulate or crenulate; living lamina pale blue-green, dull; sporophore commonly twice as long as sterile lamina; plants of eastern North America.....*B. matricariifolium*
   2. Sterile segment short-stalked or subsessile, the stalk 5–20% of the blade length; segment tips usually entire, repand, or pointed; living lamina color various; sporophore usually only 1.5 times as long as sterile segment (except in *B. hesperium*); plants of western North America.
      3. Pinnae and lobes well separated, not approximate or overlapping, mostly more or less parallel-sided, linear to oblanceolate; pinna tips pointed; basal pinnae, except in the smallest and largest fronds, usually deeply cleft into a single lower projection and larger upper projection; lamina shiny green in life.....*B. echo*
      3. Pinnae and lobes usually approximate or overlapping, the large ones abruptly contracted at base, oblong-lanceolate to ovate to deltate; pinna tips blunted or rounded; basal pinnae not cleft into two projections; color and luster various.
         4. Pinnae with few lobes, these mainly on the basal side; lowest pinnae exaggerated, ascending and subclasping, strongly asymmetrical, the lower side with coarse basiscopic lobe; segments broadly adnate at base; lamina gray-green, dull in life.....*B. hesperium*
         4. Pinnae with numerous lobes, these roughly equal in number on the upper and basal sides; lowest pinnae mostly equal to or slightly larger or smaller than next distal pair, not ascending or clasping, nearly symmetrical, the lower side with small lobes subopposite to those on upper side; segments narrowly adnate at base; lamina bright green, shiny in life. *B. pinnatum*

The following descriptions have been condensed to emphasize the most important differences between the species.

Botrychium echo W. H. Wagner, sp. nov. **Figs. 2–5.**

Sporophorum segmento sterili plerumque sesquilongius; segmentum sterile vivum supra vivide viride nitidumque, fere sessile vel brevissime stipitatum, lamina late oblonga 2.2 (1–4.5) cm longa; pinnae bene separatae, non imbricatae, oblanceolatae, lanceolatae, vel lineares, apicibus acutis, basibus subzygomorphis; pinnarum par infimum longitudine par proximum aequans vel paulo superans, patens, non amplectens; sporae tenelle verrucatae.

Plants exclusive of their roots 9.5 (3–15) cm tall, the common stalk 6 (2–10) cm tall, sporophore relatively short, 3.5 (1.5–8) cm tall, only half again as long as the sterile segment and only 20% with 1 or more branches ⅓ or more as long as main axis of sporangial cluster; sterile segment bright green and shiny in life, nearly sessile to short-stalked, broadly oblong, 2.2 (1–4.5) cm long; pinnae narrowly attached to a relatively narrow rachis, remote to approximate, not overlapping, lanceolate to oblanceolate to linear with pointed apices, the pinna bases subsymmetrical, the laminar margins nearly entire; basal pinna pair not exaggerated in length, equal to or somewhat longer than the adjacent pair, spreading or only moderately ascending, not clasping; spores 37 (27–53) μm in maximum diameter, irregularly and finely verrucate, the warts small, low, and separated by narrow, shallow channels.

TYPE: Glacier Lake, Boulder Co., Colorado, 2800 m. alt, *E. Bethel & I. W. Clokey 3937a* (US; isotypes CAS, WTU).

PARATYPES:

ARIZONA: Apache Co.: White Mts., Mt. Baldy, on open bald, *Wagner 82101* (MICH). **Coconino Co.:** San Francisco Mt., Inner Basin, *E. L. Little, Jr. 4741* (US—mixed with *B. lunaria*); NE slope of

FIG. 3. Silhouettes of moonworts. FIGS. a–e. Unusually dissected forms of *B. echo* resembling *B. matricariifolium (Wagner 82101*, MICH—see also *Fig. 1*, j). FIG. f. Probable *B. lanceolatum* × *minganense* hybrid; note the few, long segments (*Wagner 82121*, MICH). FIGS. g–i. Probable *B. echo* × *minganense* hybrids; note the relatively more numerous, shorter segments (*Wagner 82104*, MICH).

Mt. Doyle, *Wagner 82107b* (MICH). **COLORADO: Boulder Co:** Glacier Lake, July 1914, *E. Bethel* (US), 13 July 1912, *E. R. Cross* (US), *Bethel & Clokey 3987* (UC—2 sheets, both mixed with *B. hesperium*); Arapahoe Moraine, E slope, 1 mi S of University Camp, *W. A. Weber 3431* (WTU). **Clear Creek Co.:** Roadside near Echo Lake, *Wagner 80136b* (MICH), *81153b* (MICH); Warren Mt. Picnic Ground, 2.8 mi E of CO-515, *Wagner 81158* (MICH); US-6, 0.8 mi S of I-70, *Wagner 81160* (MICH). **El Paso Co.:** Pikes Peak below moraine, *H. L. Shantz 52* (US). **Gunnison Co.:** Monarch Pass, *Wagner 82118* (MICH); 0.5 mi E of Monarch Pass on CO–50, *Wagner 82123* (MICH). **Lake Co.:** Road to Independence Pass, 3.1 mi E of Hairpin Turn, *Wagner 82127* (MICH). **Summit Co.:** Near Breckenridge, *K. K. Mackenzie 99* (NY—mixed with *B. lanceolatum*); CO-91, 2–3 mi S of I-70, *Wagner 81164* (MICH). **UTAH: Summit Co.:** 1.5 mi S of Spirit Lake, *A. H. Holmgren et al. 7130* (UC—mixed with *B. lunaria*).

The Greek specific epithet *echo* is used here in apposition. It was chosen to reflect the fact that this moonwort seems to repeat the characteristics of other, similar species. One of the best areas to study it is where we first recognized its distinctions from *B. hesperium*, namely Echo Lake on the slopes of Mount Evans, Colorado.

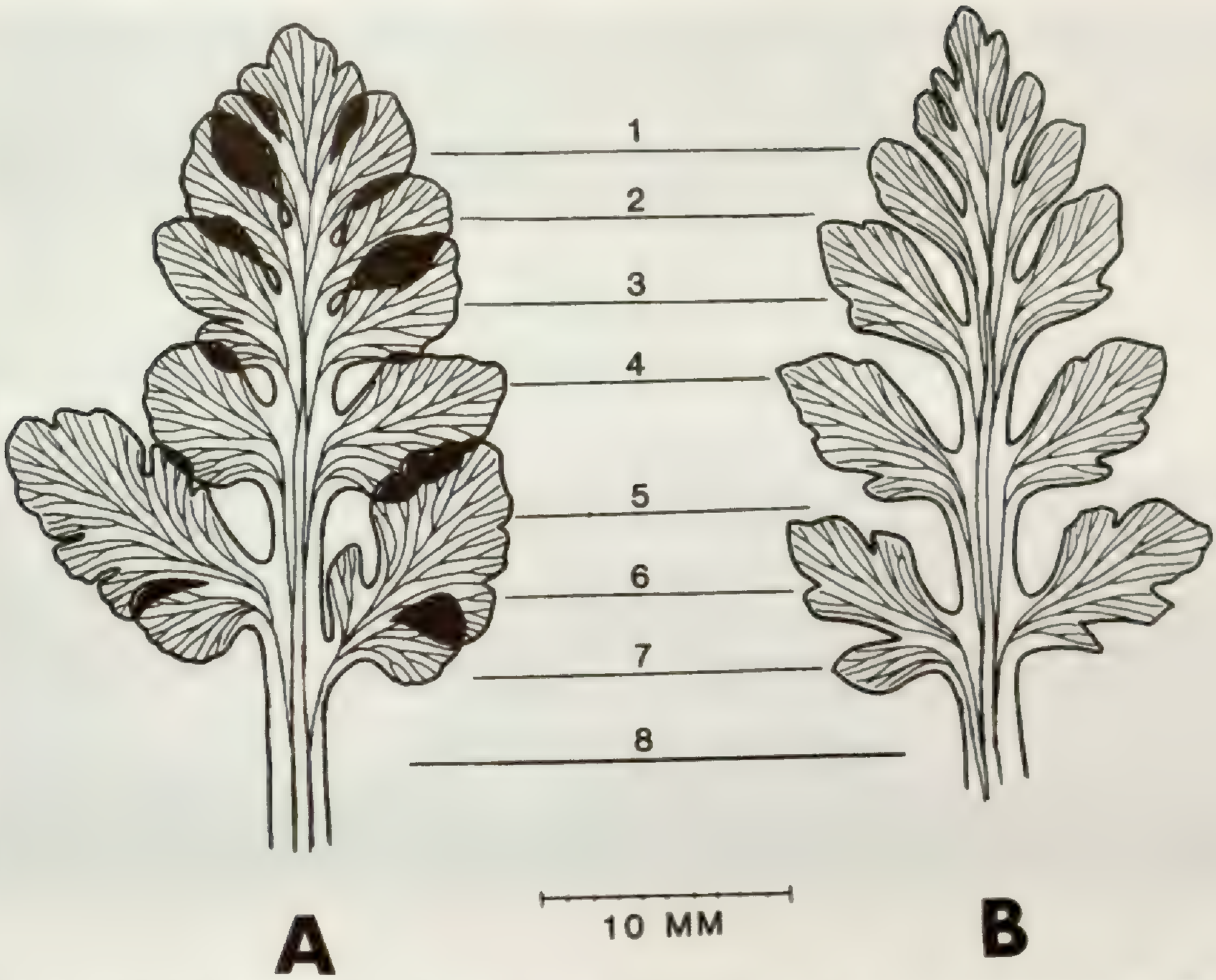

FIG. 4. Comparison of *B. hesperium* (A) and *B. echo* (B) from a mixed population at San Francisco Peaks, AZ. Tracings of cleared sterile blades. The characters are: 1 = ovate, broadly attached vs. linear-lanceolate, narrowly attached pinnae. 2 = Overlapping vs. separated pinnae. 3 = Repand vs. subentire margins. 4 = Rounded vs. pointed pinna tips. 5 = Basal pinnae much larger than vs. subequal to adjacent pinnae. 6 = Basal pinnae erect and subclasping vs. spreading and non-clasping. 7 = Basal pinnae with broad, overlapping basal lobe vs. with narrow separated basal lobe. 8 = Stalk long vs. short.

In certain respects, especially the shape of the pinnae and the glossy laminar surfaces, *B. echo* resembles *B. lanceolatum*. We have not yet detected any hybrids between the two species, but they might readily be confused with one or the other of the parents.

A distinctive but uncommon form of *B. echo* with more dissected pinnae than normal is known (*Fig. 1*, j; *Fig. 3*, a–e). The basal pinnae and sometimes the medial pinnae possess 3 or 4 lobes on the lower side and 2 or 3 lobes on the upper side. Comparison of the outline of these with *B. matricariifolium* (*Fig. 1*, h–n) shows considerable resemblance. Clausen (1938), who combined *B. echo* and *B. hesperium* as a single taxon, surely had such plants as these in mind when he wrote that some specimens "can be matched almost exactly by material of [typical *matricariifolium*]." The dissected form is especially well developed at Mount Baldy, White Mountains, Arizona. It is connected by intermediates to the normal form.

Botrychium hesperium (Maxon & Clausen) Wagner & Lellinger, Amer. Fern J. 71:92. 1981, pro hybr.

Botrychium matricariifolium subsp. *hesperium* Maxon & Clausen, Mem. Torrey Bot. Club 19:88. 1938.

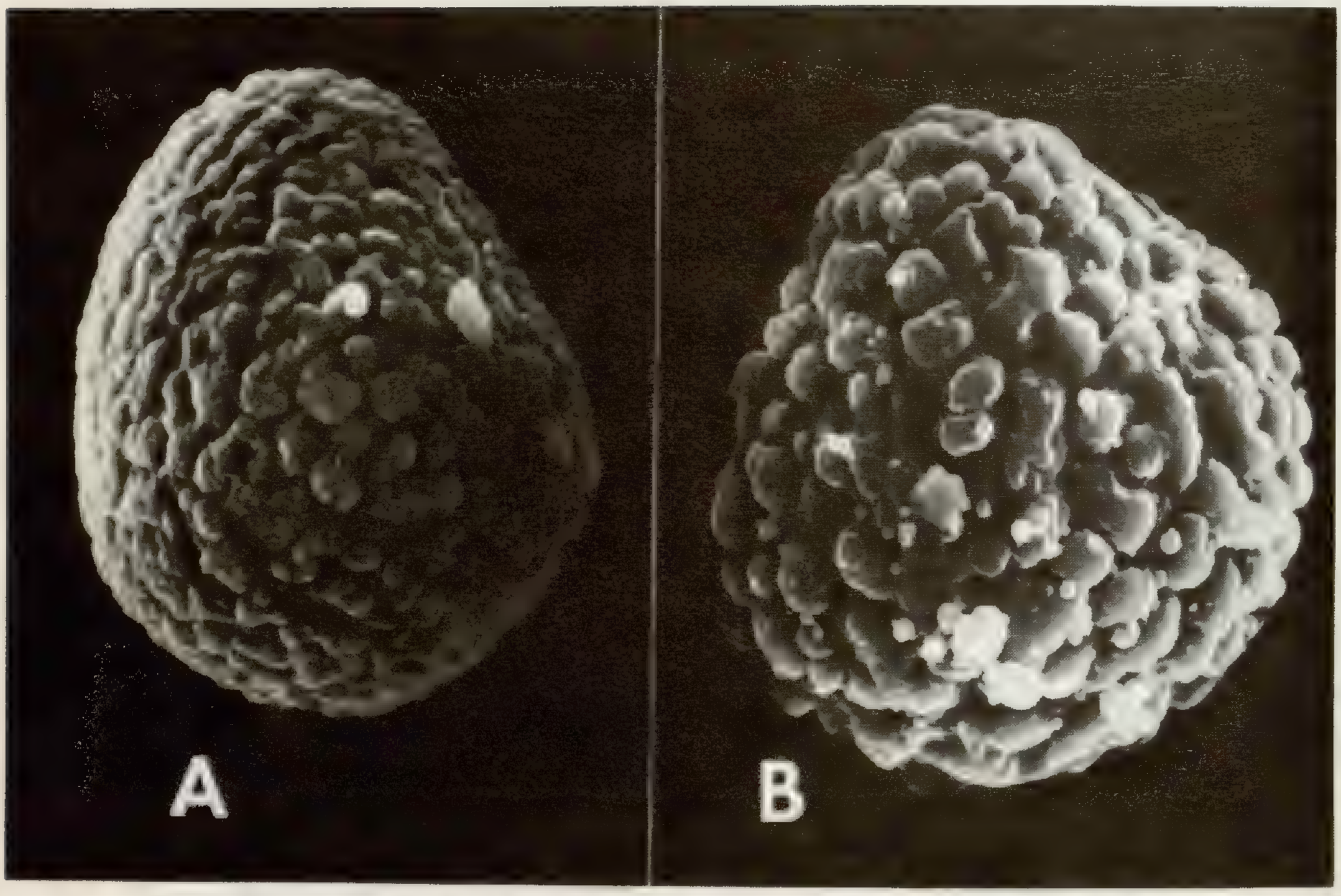

FIG. 5. Spores of *B. echo* (A) and *B. hesperium* (B). SEM photographs ×1,100. Note the differences in size and form of the verrucae.

Plants exclusive of their roots 12 (5–20) cm tall, the common stalk 7 (3–13) cm tall, sporophore relatively tall, 5 (3–10) cm tall, nearly twice as long as sterile segment, 80 percent with 1 or more basal branches ⅓ or more as long as main axis of sporangial cluster; sterile segment gray-green and dull in life, mostly short-stalked, subdeltate, 2.5 (1–5) cm long; pinnae broadly attached to a relatively wide rachis, crowded to commonly overlapping, ovate to lanceolate with rounded apices, the pinna bases asymmetrical, the lamina margins finely repand; basal pinnae commonly exaggerated, up to twice as long as the adjacent ones, often upright and commonly clasping; spores 37 (29–50) μm in maximum diameter, irregularly and coarsely verrucate, the warts large, prominent, and separated by wide, deep channels.

TYPE: Glacier Lake, Boulder Co., Colorado, 8500 ft, July 1914, *E. Bethel* (US—5 isotypes in addition).

OTHER COLLECTIONS EXAMINED:

CANADA: Alberta: Waterton Lakes National Park, W of Red Rock Canyon Parking Area, *Wagner 81103a-d* (MICH).

ARIZONA: Coconino Co.: San Francisco Peaks, Inner Basin, NE slope of Doyle Mt., *Wagner 82107a* (MICH). **COLORADO: Boulder Co.:** Glacier Lake, *Bethel & Clokey 3987* (CAN, CAS, US); Rocky Mt. National Park, Loch Vail Trail, Glacier Gorge, *A. E. Porsild & B. E. Willard 23102* (CAN). **Clear Creek Co.:** Roadside near Echo Lake, *Wagner 80136a* (MICH), *81153a* (MICH). **Lake Co.:** Road to Independence Pass, 3.1 mi E of Hairpin Turn, *Wagner 82128* (MICH). **MONTANA: Deer Lodge Co.:** Flint Ridge Mts., Storm Lake, S of Georgetown Lake, *Wagner 80129a* (MICH), *81116b* (MICH).

It is interesting to note that Maxon's original, unpublished interpretation of this taxon was as given here. On the type specimen he had written the label to read "Botrychium hesperium Maxon sp. nov." The occurrences that we have found so far

in Montana and Alberta contain plants much smaller on the average than those in Colorado and Arizona. The northern plants resemble young stages of the southern ones, and they may be dwarfed by the climate. The coarsely sculptured spores that we observed in *B. hesperium* (*Fig. 5*, B) are like those of *B. lanceolatum*.

For *B. echo*, our collection records range from 13 July to 20 September, with most specimens taken in August. *Botrychium hesperium* may be similar, but there is some evidence that it may appear earlier and die down earlier. Judging from the condition of the large sample of plants taken at San Francisco Peaks, *B. hesperium* shows more effects of ageing. Seventy percent of the specimens of *B. hesperium* collected on 21 August 1982 showed evidence of damage—browned margins and broken, eaten, or otherwise tattered pinnae—compared to only 30% of *B. echo* collected at the same place and time. The leaves of *B. echo* appeared to be fresher.

As would be expected, sterile interspecific hybrids involving both *B. hesperium* and *B. echo* have been encountered. Their hybrid origin is deduced by their association with parents, occurrence as usually one or a few plants, morphological intermediacy, and abortion of spores.[1]

Because only a single leaf is produced per year, it is difficult to obtain cytological observations as a rule; however, Sahashi (1979) has documented irregular meiosis in a Japanese hybrid. The most obvious interspecific hybrids are those in which the parents differ strongly (e.g., the Scandinavian hybrid of *B. boreale* and *B. lunaria*). *Botrychium hesperium* hybridizes readily with *B. paradoxum* to produce very obvious intermediates, striking because one of the two sporophores is "half sterile" (Wagner & Wagner 1981; Wagner et al., 1982). We have encountered a few definite hybrids involving *B. echo*. These involve *B. minganense* Victorin. Some are from Mount Baldy, Arizona, where the parents occur together locally in abundance. At San Francisco Peaks, we found a number of sterile plants involving what appear to be combinations of *B. echo, hesperium,* and *lunaria*, but these will require more study to separate. Some hybrids involve yet other species, for instance, a specimen from Monarch Pass, Colorado, we first thought was *B. echo* × *minganense* (*Fig. 3*, f). However, the cutting is somewhat different; also *B. echo* is rare and sporadic at this locality, while both *B. lanceolatum* and *minganense* are abundant and the latter species probably are the parents.

This is part of an investigation of the evolution and systematics of *Botrychium* made possible by NSF grants DEB 800536 and DEB 8202768. We are indebted to a number of individuals who have helped us, especially W. R. Anderson, R. Eccleston, R. H. Hevly, J. Kuijt, J. D. Montgomery, A. Neas, W. A. Weber, M. D. Windham, and G. Yatskievych. The following herbaria have kindly supplied specimens of the species considered here: ASC, BRY, CAN, CAS, DAO, MO, NY, UC, US, and WTU.

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[1]Confirmation of spore abortion is accomplished in *Botrychium* using only a dissecting microscope at 30–60X magnification. The spores of specimens that were dried while the sporangia still had not completely discharged tend to be released and become attached (electrostatically?) to the sporophore axes and opened sporangial walls. If the spores are abortive, the sizes are extremely irregular—very small, normal, and very large. The largest spores tend to be more or less spherical and not tetrahedral.

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SHORTER NOTES

LYCOPODIUM COMPLANATUM AND L. ANNOTINUM FOUND IN THE BLACK HILLS.—*Lycopodium complanatum* L. and *L. annotinum* L. were found growing together in the Black Hills of Wyoming on July 27, 1982. The location is in Crook County, Upper Sand Creek at confluence with Spottedtail Gulch, T51N R60W Section line of 20–21, elevation 5600 feet. The plants were growing under White Spruce, *Picea glauca* (Moench) Voss, and Hazelnut, *Corylus cornuta* Marsh., along with Low Red Huckleberry, *Vaccinium scoparium* Leiberg. *Lycopodium complanatum* was found only at this location, but *L. annotinum* extended on down the canyon at several more localities. Specimens are deposited at the University of Wyoming (RM) and the New York Botanical Garden (NY) (*Dorn 3793, 3792*). The closest known locality for *L. complanatum* is about 450 miles to the northwest in Lewis and Clark County, Montana. The closest known locality for *L. annotinum* is about 270 miles to the west in Park County, Wyoming.

Several other pteridophytes were collected within two miles of the *Lycopodium* location along the same creek: *Equisetum sylvaticum* L. (*Dorn 3777*, collected for the first time in Wyoming one day earlier by E. F. Evert in the Big Horn Mountains), *Athyrium filix-femina* (L.) Roth (*Dorn 3778*), and *Equisetum scirpoides* Michx. (*Dorn 3809*, another first record for Wyoming).—*Robert D. Dorn, Box 1471, Cheyenne, WY 82003.*

MICROFIBRILS IN THE XYLEM OF BLECHNUM VIVIPARUM. — Cellulose forms the framework of plant cell walls by a system of microfibrils (as well as other molecular shapes) in which various substances are incrusted. The presence of microfibrils can be demonstrated by chemical removal of the incrusting substances or, rarely, by their actual appearance in the lumen of pits, particularly in relation to tori and plasmodesmata of some angiosperms and conifers. After the formation of secondary walls in some Gnetaceae and Coniferae (Warchop et al., Holzforsch. 13:115–120. 1959), a sort of "tertiary growth" appears in the shape of warts or of fibrils, either isolated, at random, or in a margo (a marginal reticule that fuses at or near the center of the torus), and sometimes obliterates the lumen (Butterfield & Meyland, Three-dimensional Structure of Wood, p. 72. 1980).

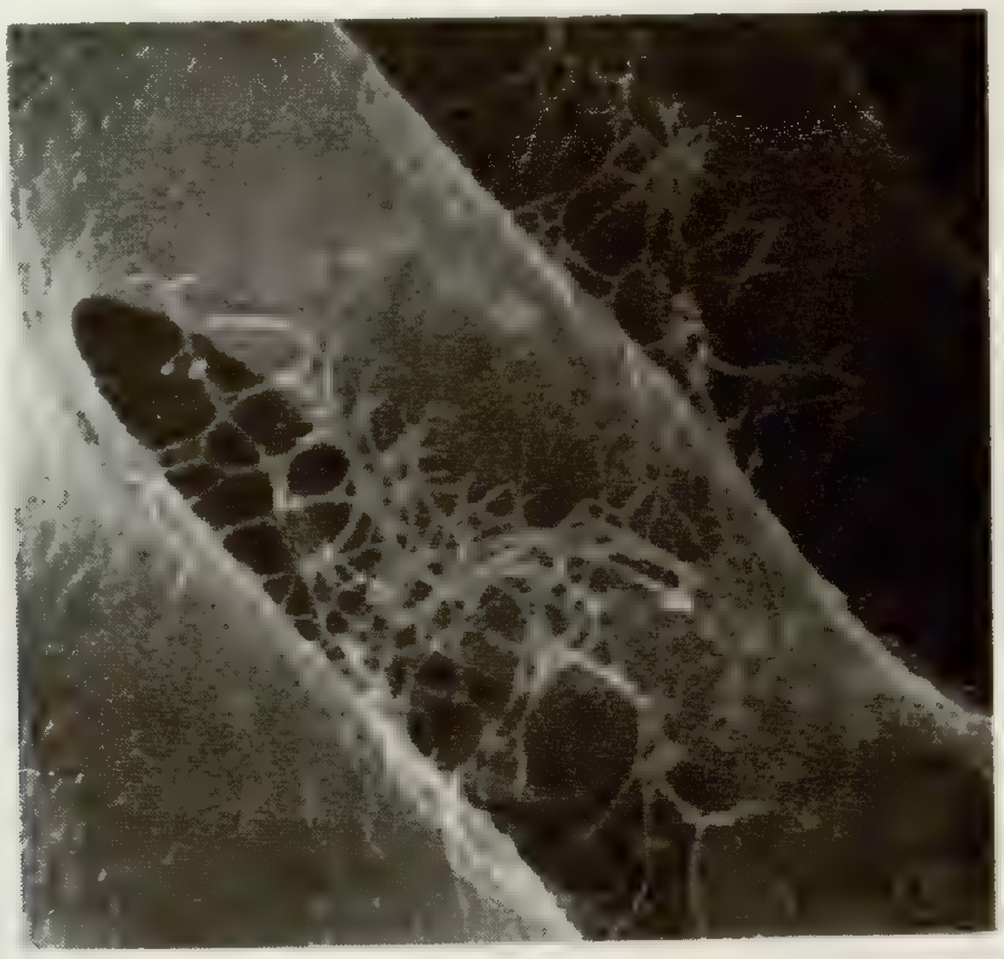

FIG. 1. Isolated, sporadic xylem elements in *Blechnum viviparum* interpreted as secondary vessels. Two pits showing a loose net of microfibrils, ×10,000.

In the material of *Blechnum viviparum* (Broadh.) C. Chr. studied and reported by Montiel and Guevara (Rev. Biol. Trop. 27:171–176. 1979) and reinterpreted by Gómez (Brenesia 18:253–258. 1980), some of the pits show what in my opinion are microfibrils (*Fig. 1*) which, to my knowledge, have either been overlooked or have not yet been reported from vascular cryptogams where xylem elements or secondary growth have been detected. It must be pointed out that the microfibrils reported here seem somewhat thicker than those usually found in higher plants and, unlike those, ours are sporadic and quite scattered throughout the material.

The presence of microfibrils in ferns is interesting from a phylogenetic point of view inasmuch as they represent another intermediate character between the tracheid and the coniferophyte-type element. Furthermore, the presence of loose microfibrils partially obliterating the lumina between crassulae, projecting from the middle lamellae to the secondary walls in a pteridophyte, seems to support the idea of a coherent, organized constitution of cellulose in the primary membranes as proposed by Frey-Wyssling et al. (Planta 47:115–126. 1956) and Mühlethaler (Biochem. Biophys. Acta 5:1–9. 1950), at least in these primitive plants.—*Luis D. Gómez P., Museo Nacional de Costa Rica, Apartado 749, San José, Costa Rica.*

BISPORANGIATE ANOMALOUS SPOROPHYLLS IN ISOËTES FROM RAJASTHAN—The presence of a solitary, adaxial sporangium on or in association with a sporophyll is the fundamental feature of all lycopods. Only two exceptions have been reported. The fossil *Lycostachys protostelicus* was described by Pant and Walton (Palaeontographica 108:1–10. 1961) as having two subarchesporial pads in a sporangium; and in *Isoëtes indica,* Pant and Srivastava (Proc. Natl. Inst. Sci., India, B, Biol. 23:242–280. 1962) described sporophylls having two, almost equally developed sporangia. The discovery of bisporangiate sporophylls in two additional species of *Isoëtes*, *I. coromandelina* L. f. collected at Poasa near Jaipur, Rajasthan, and in an apparently new species of *Isoëtes* from Mt. Abu, Rajasthan, India, are additions to this list.

FIG. 1. Bisporangiate, abnormal sporophylls of *Isoëtes coromandelina,* ×1.2. FIG. 2. Longisection of bisporangiate sporophyll of *Isoëtes* sp. from Mt. Abu showing two unequal sporangia, ×20.

A number of abnormal sporophylls were discovered in *I. coromandelina* which possess double sporangia (*Fig. 1*). These seem to be produced by fusion between adjacent sporophylls during their development. The proximal portions of the sporophylls are united and bear two sporangia; the distal, acicular portions of the sporophylls are free. The ligules and upper labia are also double. However, in other details of morphology and anatomy the sporophylls are normal.

In the *Isoëtes* from Mt. Abu, an abnormal sporophyll bearing two sporangia was discovered during sectioning of the material. The two sporangia are unequal and are separated by a partitioning wall (*Fig. 2*). The smaller sporangium is empty and seems to be a bud-like, sterile structure; the bigger one is normal and contains numerous megaspores.

From the present discovery, it seems that double sporangia are not so rare in *Isoëtes*. Further investigations are needed to establish any possible phylogenetic conclusions.—*B. D. Sharma, R. Singh,* and *D. R. Bohra, Department of Botany, University of Jodhpur, Jodhpur 342001, India.*

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Observations on the Structure and Function of Hydathodes in Blechnum lehmannii

JOHN S. SPERRY*

The fronds of many ferns in the Polypodiaceae (Ogura, 1972) and Cyatheaceae (Weiler, cited in Lippmann, 1925) possess swollen vein endings associated with specialized adaxial epidermal cells. Their structure is similar in all ferns (Gardiner, 1883; Potonié, 1892; Poirault, 1893; Goebel, 1930; Guttenburg, 1934), including *Blechnum lehmannii* Hieron. (*Figs. 1–3*). The depressed epidermis (*Fig. 3*) suggested the term "Wassergrübchen" for the vein endings to European anatomists of the nineteenth century (e.g., Potonié, 1892). Vein endings on developing fronds secrete water (*Fig. 1*) when conditions reduce or stop transpiration (Mettenius, 1856; Haberlandt, 1894a; Goebel, 1926, 1930). In some species, the secreted water contains salts in solution which form "chalk scales" after the water has evaporated (Mettenius, 1856; Potonié, 1892; Lippmann, 1925).

Most sources report that water secretion is dependent on the metabolic activity of the specialized epidermal cells adaxial to the vein ending (*Fig. 3*, e); it is thus regarded as an active, or glandular, process (Gardiner, 1883; Haberlandt, 1894a, 1914; Lepeshkin, 1906; Stocking, 1956; Fahn, 1979). This conclusion is reflected in various references to the vein endings as water glands, salt glands, or chalk glands. There is, however, very little evidence to support any conclusions on the mechanism of secretion. All work on the subject was performed in the last century, and the results obtained are questionable due to the bias in experimental design which prevented testing of alternative hypotheses and to the possibility of artifacts in technique (see comments in Spanjer, 1898; Haberlandt, 1898; Lepeshkin, 1923). Moreover, the results are contradictory, since they have been interpreted as supporting either an active (Gardiner, 1883; Haberlandt, 1894a, 1914) or a passive (Spanjer, 1898) mechanism of secretion. Finally, all experiments were performed on a single species, *Polypodium aureum* L., and need not represent the situation in other ferns.

Because the mechanism of secretion from vein terminations is unknown, they will be referred to in this paper by the term "hydathode" which, as originally defined by Haberlandt (1894b), did not presuppose a mechanism of secretion. Haberlandt used his term to refer to structures on above-ground portions of the plant, particularly foliage leaves, which function in water transfer to and from the plant surface.

Previous work on the mechanism of hydathode secretion in ferns neglected important aspects of the problem. Despite the fact that root pressure could play a significant role in the secretion process, the relationship of root pressure to secretion in intact plants was not studied. In fact, there is no well documented account of root pressure in ferns. In addition, investigators could not analyze secretion from a structural standpoint because anatomical studies were confined to the mature, non-secreting hydathodes; the structure of the secreting hydathodes on developing leaves was unknown. In this study, the relationship of root pressure to secretion as well as developmental changes in hydathode structure were investigated in *B.*

* Harvard Forest, Petersham, MA 01366.
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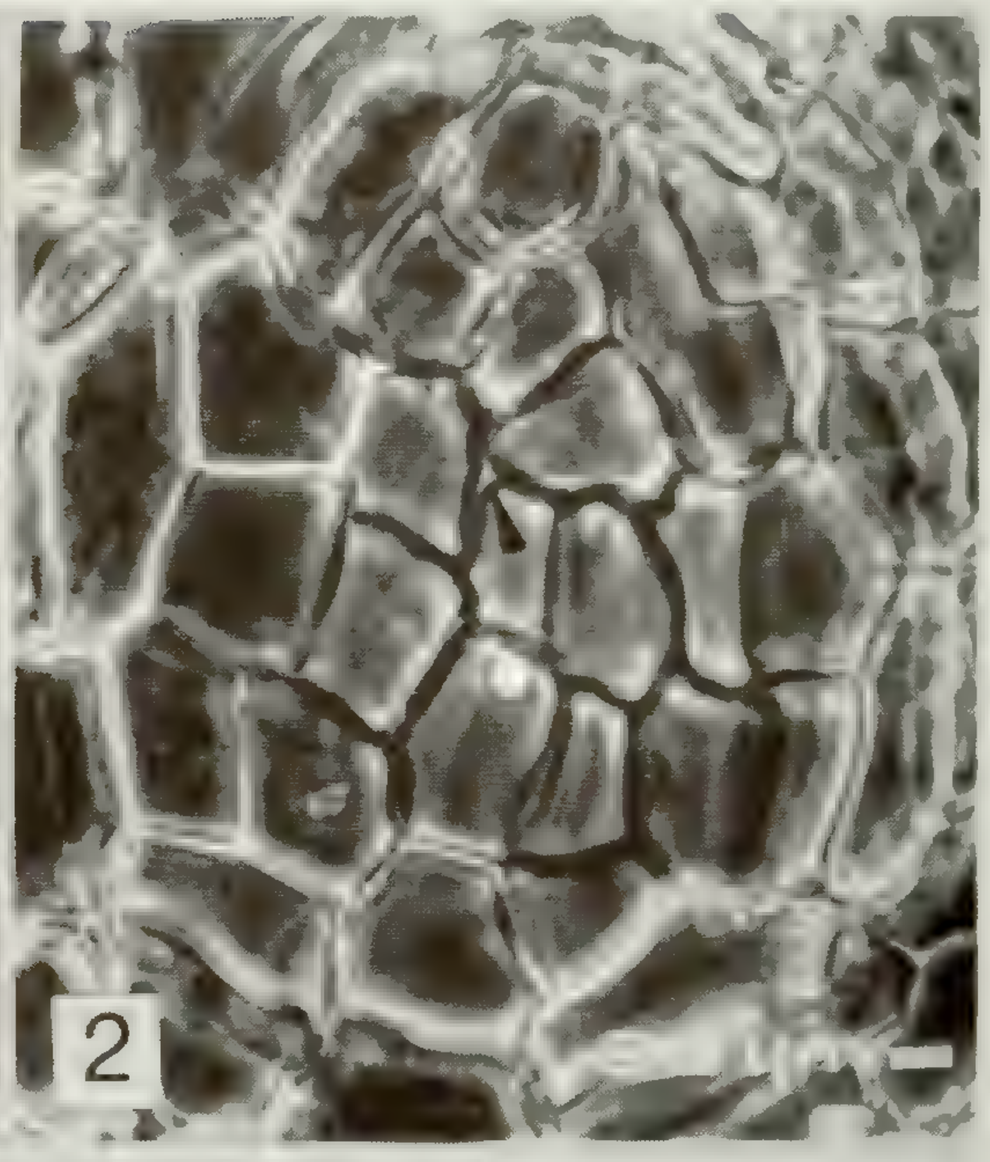


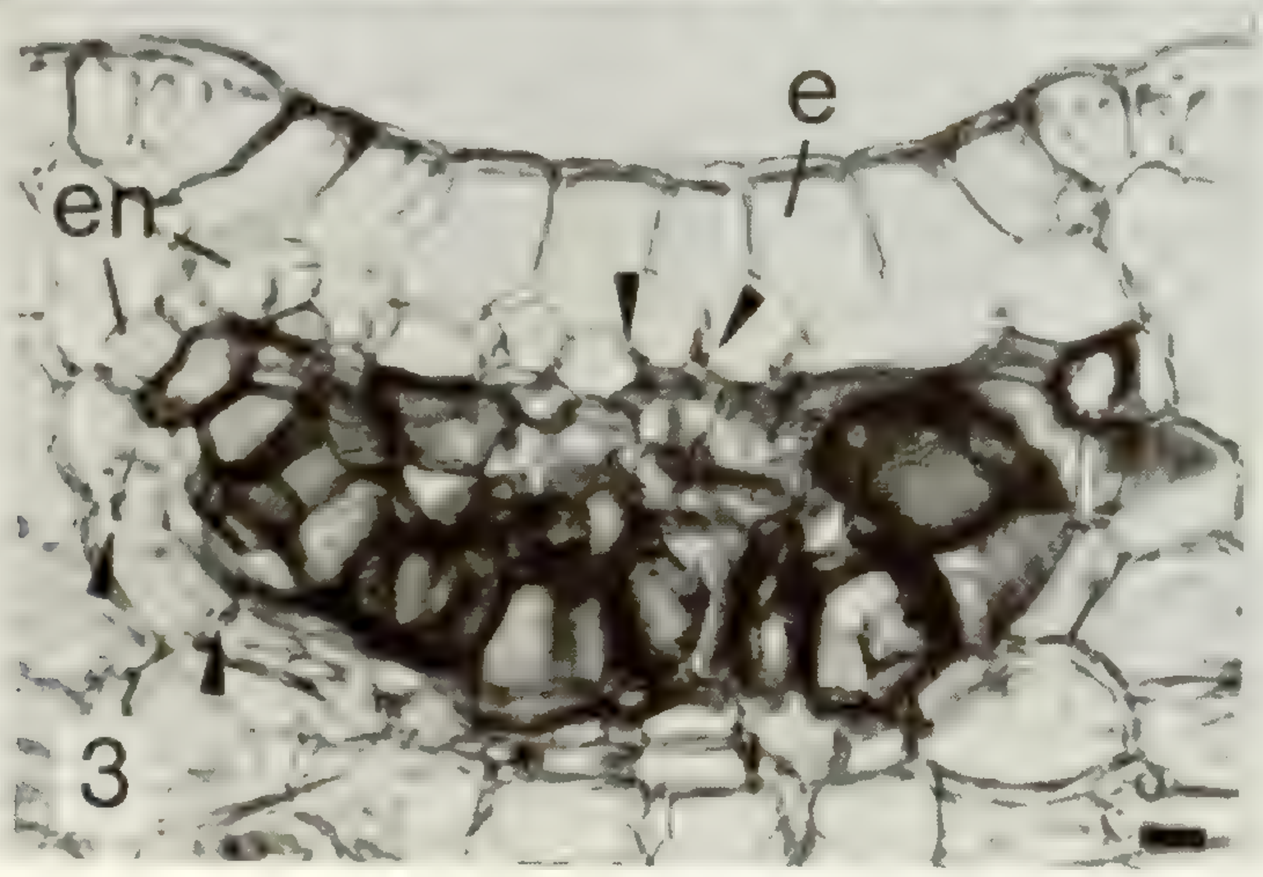


FIG. 1. Hydathodes secreting water on a developing frond; arrow indicates a droplet of water above a hydathode. FIG. 2. Epidermal peel of hydathode photographed with dark field illumination. There is no intercellular space in the epidermal layer; the separation of cells marked by the arrow is an artifact of preparation due to the weak adherence between epidermal cells. FIG. 3. Transverse section of a hydathode on a mature frond made parallel to the leaf margin and treated with I-KI/H_2SO_4. e = epidermal cells of hydathode, en = endodermis; arrows indicate Casparian strip.

lehmannii in its native locality, the Central American cloud forest. Observations suggest that one mechanism of secretion from fern hydathodes is the passive transmission of xylem sap from vein endings to the plant surface through the apoplast of the hydathode under a pressure gradient induced by root pressure.

MATERIALS AND METHODS

Plants growing in the cloud forests near Xalapa in the state of Veracruz, Mexico; provided material for both experimental and anatomical work. Individual plants consist of a single, erect rhizome with short internodes.

Root pressure was measured with a bubble manometer attached to the cut stipe (*Fig. 4A*) and a thermometer. The manometer was made with surgical tubing (ca.

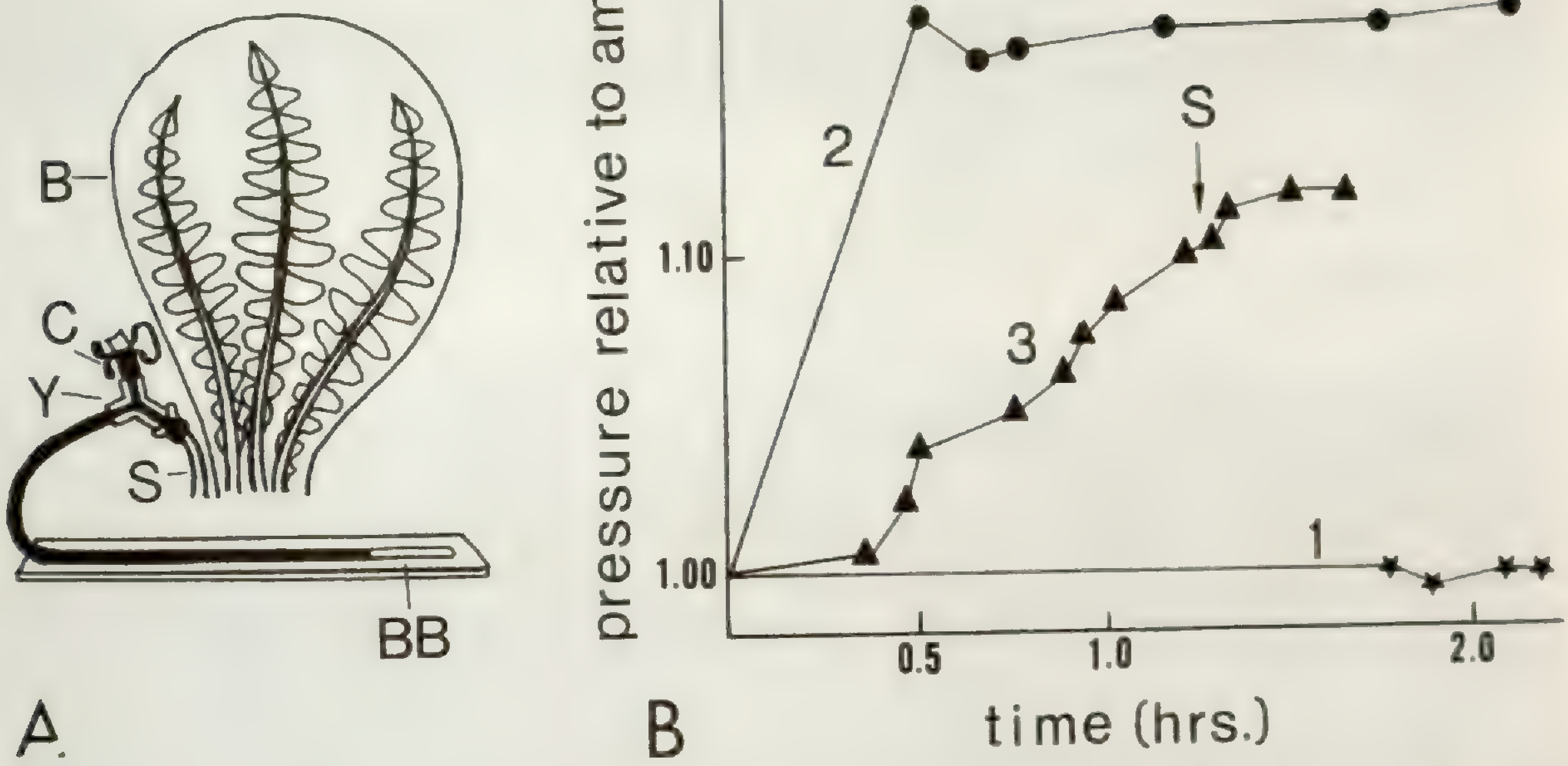
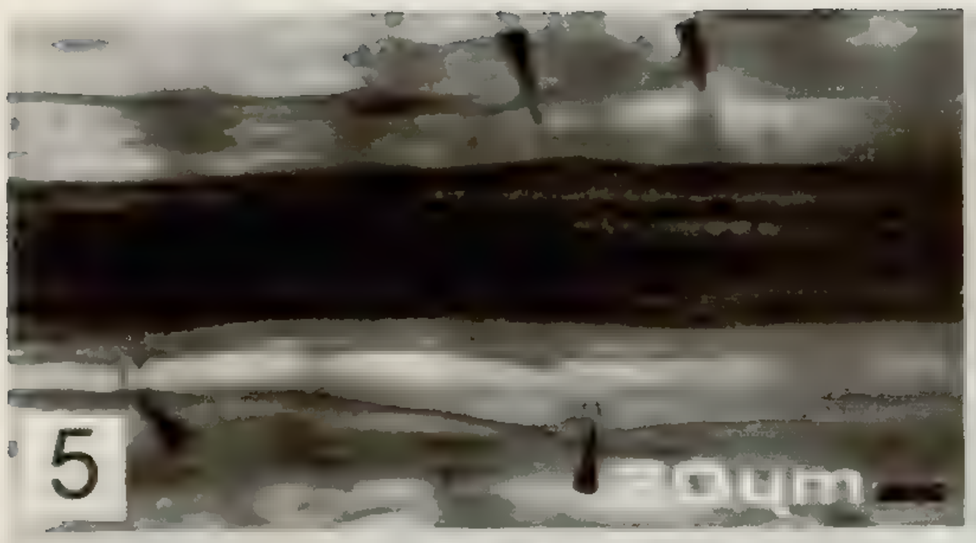


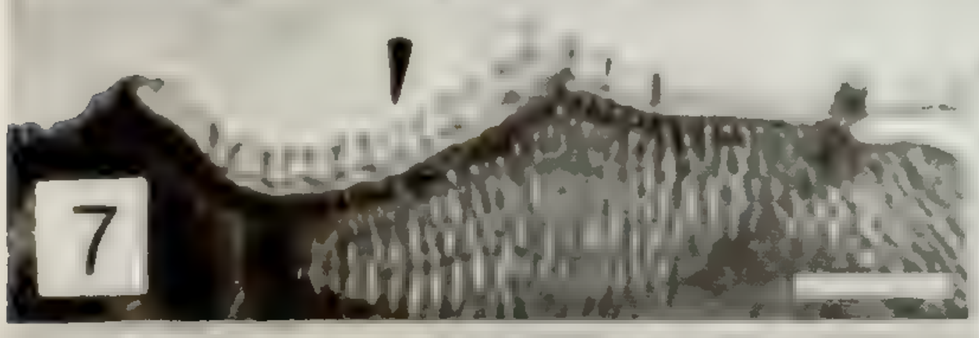
FIG. 4A. Manometer attachment for measuring root pressure. B = clear plastic bag enclosing the entire crown of an individual plant, S = cut stipe to which the manometer is attached, C = clamp, Y = forked connector, BB = bubble at sealed end of the manometer tube. FIG. 4B. Root pressure vs. time for plants 1, 2, 3. S = onset of hydathode secretion.

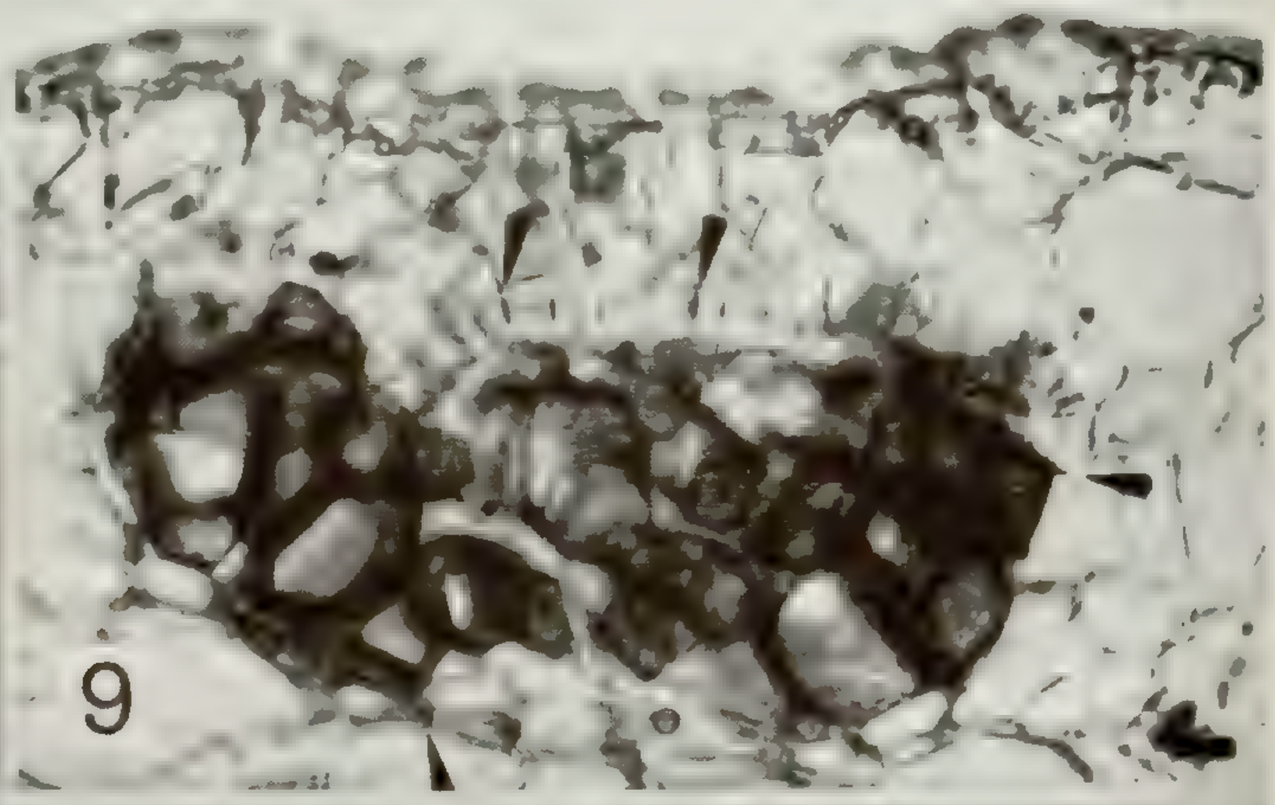
0.8 mm inside diameter) partially filled with acid fuchsin and sealed at one end so as to leave a bubble at the sealed end (*Fig. 4A*, BB). Bubble length was assumed to be proportional to bubble volume. At the beginning of the experiment, bubble length at ambient pressure and air temperature was determined by releasing the clamp (*Fig. 4A*, C). After the clamp was closed, subsequent readings of bubble length and air temperature were made, and exudation pressure relative to ambient was calculated according to Gay-Lussac's law (Weast & Astle, 1981). Clamping itself did not affect bubble length. Care was taken when attaching the manometer so that a continuous column of liquid was present from stipe to bubble, and the attachment was gently secured with twist-ties to help guard against leakage.

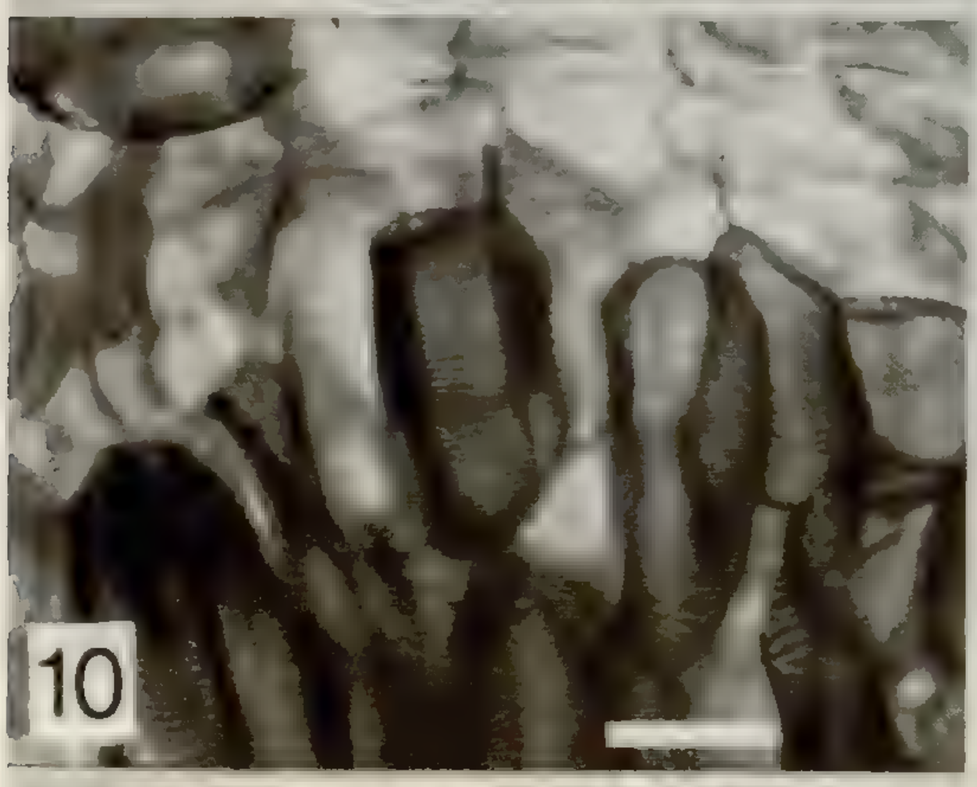
The relationship between root pressure and hydathode secretion was studied in three plants growing along a shaded stream in the cloud forest on a clear day. The entire above-ground portion of each individual plant was enclosed in a clear plastic bag and root pressure was monitored with a manometer attached to a single cut frond for each plant (*Fig. 4A*). Observations of xylem pressure and hydathode secretion were then made.

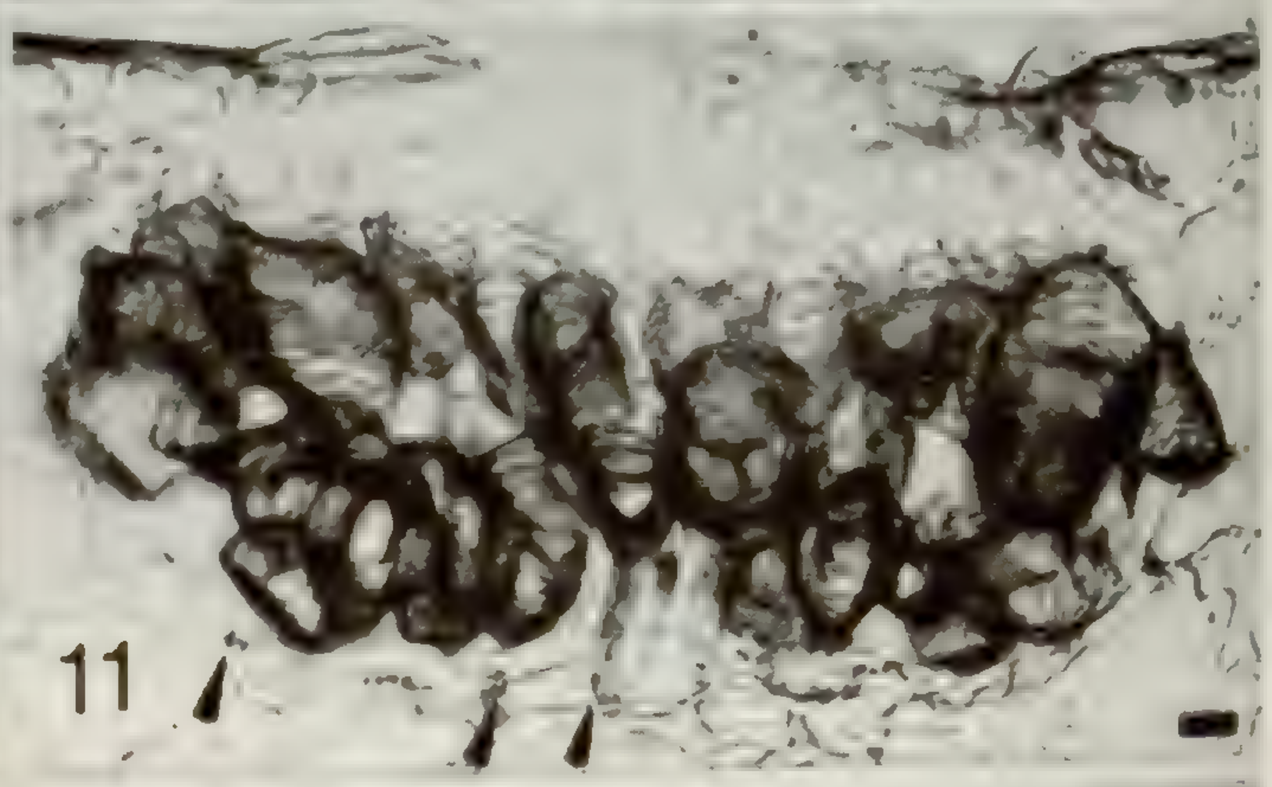
Anatomical differences between the secreting and non-secreting hydathodes on these three plants and others were studied from hand sections and clearings from both fresh and material fixed in FAA. Clearings were made by treating the leaf with alcoholic sodium hydroxide followed by lactic acid. Observations were made on preparations left unstained or stained in toluidine blue. The distribution of lignin was determined from hand sections stained in phloroglucinol and concentrated HC1. Suberized and cutinized cell walls were identified using the I–KI/H_2SO_4 test.

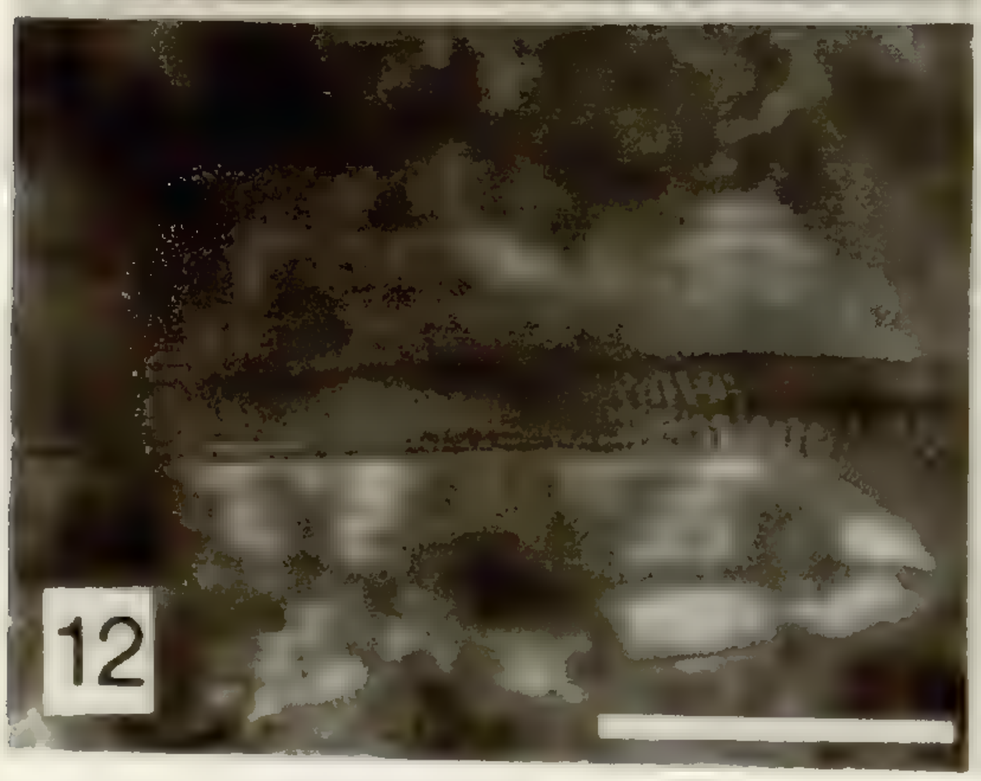












FIGS. 5–13. Development of Casparian strip. All preparations were treated in I–KI/H_2SO_4. FIGS. 5–8, 10, and 12 are from cleared preparations; FIGS. 9, 11, and 13 are transverse sections made parallel to the leaf margin. Arrows = Casparian strip. FIGS. 5–9. Non-secreting hydathodes on mature frond. FIG. 5. Vein subtending a hydathode and surrounded by endodermis with fully developed Casparian strip. FIG. 6. Hydathode viewed from the adaxial epidermis and focussed on the Casparian strip bordering the edge of the vein ending. FIG. 7. Higher magnification of the Casparian strip as viewed in

OBSERVATIONS

Secretion.—Secretion was observed on developing, unenclosed fronds in foggy and rainy weather in the cloud forest and when individual crowns were enclosed in plastic bags. In bagged plants, secretion was initiated on successive pinnae in an acropetal direction so that the last hydathodes to begin secreting on developing fronds were those on the most distal pinnae. Based on qualitative observations, distal hydathodes appeared to have a greater rate of secretion than more proximal hydathodes, which on developing fronds sometimes showed no secretion. Observations of fronds at different stages of development as judged by relative size, color, and texture suggested that the permanent loss of secreting capability by hydathodes occurs acropetally. No salt deposits of any kind were observed to accumulate above the hydathodes.

Root pressure.—Root pressure was determined by examining the bleeding behavior of cut stipes (*Fig. 4A*, S) on plants growing in conditions which were assumed to severely reduce or stop transpiration. Such conditions were either natural, as on rainy or foggy days, or induced by enclosing the entire above-ground portion of an individual plant in a clear plastic bag (*Fig. 4A*, B). Root pressure was assumed to be present when the attached stipes showed continual bleeding after being cut. Initially, some of this bleeding was due to mucilage flow as judged by the viscous nature of the exudate. However, after continual blotting over a period of several minutes, the viscosity of the bleeding fluid decreased considerably, and with the aid of a hand lens, xylem sap could be seen issuing from the stele. Plants in which transpiration was not inhibited did not show this bleeding behavior from cut stipes; here the only exudation noted was a small amount of mucilaginous material.

Although the secretion of mucilage from the cut end of the stipe was a potential problem for root pressure measurements, the results indicate that the pressure produced by the secretion is insignificant. Certain plants (e.g., plant 1, *Fig. 4B*) did not show root pressure even when transpiration was reduced by enclosure of the crown in a plastic bag. The absence of root pressure in these plants was apparently due to insufficient soil moisture. Despite the fact that the stipes of these plants showed mucilage secretion when cut, no significant increase in pressure above ambient was noted from attached manometers.

The relationship between root pressure and hydathode secretion studied in the three bagged plants (labelled 1, 2, 3) is summarized in the graph of *Figure 4B*. In plants 2 and 3, the buildup of root pressure in the xylem correlated positively with the observation of water secretion from hydathodes of developing fronds. In both plants, the measured pressures were sufficient to support a column of water taller than the height of the plant (1.8 m for plant 2, 1.2 m for plant 3). Plant 1 developed

Fig. 6 but with cellulosic walls dissolved by long exposure to sulphuric acid. The Casparian strip abuts directly on the tracheids of the vein ending. FIG. 8. Casparian strip adaxial to the vein ending in surface view with cellulose dissolved. FIG. 9. Hydathode with depressed epidermis and uniform development of Casparian strip around the vein ending. FIGS. 10–13. Secreting hydathodes on developing frond. FIG. 10. Hydathode viewed as in *Fig. 6* but with no Casparian strip. FIG. 11. Slightly protuberant hydathode with Casparian strip only developed adaxially. FIG. 12. Vein subtending a hydathode and without a Casparian strip. FIG. 13. Protuberant hydathode with no Casparian strip; dark, round structures are probably phenolic vacuoles.

no root pressure, and no secretion was observed from its hydathodes.

Variation in root pressure in the three plants is correlated with position relative to the stream flowing under the bank where they were growing. Plant 2, which showed the most dramatic rise in pressure, was growing roughly 0.3 m above the stream level. Plant 1, which showed no root pressure, was 2.5 m above the stream. Plant 3 was intermediate in pressure and bank position. Possibly the explanation for this correlation is decreasing soil moisture with increasing height above the stream; greater soil moisture would favor the generation of higher root pressures.

Hydathode development.—The ability of hydathodes to secrete is correlated with specific features of their development. Hydathode cells reach their mature size and are capable of secreting water long before the cells of the surrounding leaf tissue have finished expanding. Hydathodes capable of secreting protrude above the surrounding epidermal cells (*Fig. 13*). Only after the leaf cells reach their full size and the leaf achieves its mature thickness do hydathodes become the depressed "Wassergrübchen" consistently described by early anatomists (*Figs. 3* and *9*). In the recessed stage, hydathodes were observed to be incapable of water secretion.

The structural change that appears to be most closely related to secretory function is the progressive suberization of the hydathode endodermis. The Casparian strip surrounding the hydathode (*Figs. 3* and *9*) is the distal extremity of a network which surrounds the entire mature vascular system of the plant. The development of this continuous Casparian strip is acropetal, and lags considerably behind the maturation of protoxylem and hydathode cells (*Figs. 10, 12,* and *13*). Thus, hydathodes in developing tissues do not possess a suberized endodermis.

The acropetal extension of the Casparian strip to the hydathode is first evident in the endodermis abaxial to the vein ending (*Fig. 11*, arrows). The vein subtending the hydathode is completely surrounded by a Casparian strip (*Fig. 5*). At this time, the Casparian strip around the vein ending is like a mitten with the abaxially turned palm cut out. Development of the Casparian strip proceeds with the first steps represented by thin bands of suberin extending from the well developed strip below the vein. Eventually, the abaxial endodermis of the vein ending possesses a Casparian strip as well developed as anywhere else in the frond (*Fig. 9*).

The degree of Casparian strip development at the hydathode correlates closely with the capability of the hydathode to secrete water. Examination of developing fronds from plants 2 and 3, which possessed distal secreting hydathodes and proximal non-secreting hydathodes, indicated that secretion only occurred from hydathodes where the Casparian strip was either absent or incompletely developed. In one frond, for example, distal secreting hydathodes which from qualitative observation showed the highest secretion rate possessed no Casparian strip (*Figs. 10* and *13*). Hydathodes on pinnae from the middle part of the frond, which appeared to have a lower rate of secretion, possessed an incompletely developed Casparian strip adaxial to the vein ending (*Fig. 11*). Hydathodes at the base of the frond showed no secretion and were found to be completely surrounded by a thick Casparian strip (*Figs. 6–9*). In addition, examination of fronds at different stages of Casparian strip development indicated that the acropetal progression of complete hydathode suberization correlates with the acropetal loss of secretion capability in the hydathodes.

DISCUSSION

The correlation of root pressure with secretion from hydathodes on the one hand, and the correlation between Casparian strip development and the cessation of hydathode secretion on the other, suggest a simple explanation for the occurrence of water secretion from hydathodes in *B. lehmannii*. Root pressure is directly responsible for secretion by supplying a pressure gradient sufficient to drive the passive movement of xylem sap from the vein ending of the hydathode, through the apoplast of the sub-epidermal and epidermal cells, and through the thin cuticle to the outside of the plant. When the Casparian strip is completely formed around the vein ending of the hydathode, the apoplast is sealed and secretion from the hydathode is blocked. Preliminary results from *Polypodium* and *Nephrolepis* species indicate that this hypothesis can also apply to hydathodes in these genera.

Root pressure is known to be directly responsible for secretion from the epidermal-pore hydathodes of angiosperms (Fahn, 1979). Although pores are not present in the epidermis of fern hydathodes, root pressure can move water to the plant surface through the anticlinal walls of the epidermal cells. According to Meidner (1977), root pressure causes the secretion of water from the epidermal cell walls of *Gladiolus* leaves which lack epidermal-pore hydathodes, and the same explanation may account for Goebel's observation (1930) of secretion from the blade margins of ferns without hydathodes.

The results presented in this paper do not preclude the possibility that water secretion is partially or wholly active, and more research is required to decide the question. Hydathode epidermal cells could play a role in the modification of the solute content of the secreted xylem sap. Thus, they would be analogous to glandular cells found associated with epidermal-pore hydathodes of the angiosperms (Dieffenbach, et al., 1980). If the epidermal cells are capable of secreting salts, there may also be a metabolically dependent osmotic mechanism which contributes to water secretion, at least for those fern species that characteristically secrete large amounts of salts and form "scales" (see Lepeshkin, 1906). Regardless of the specific mechanism of secretion, however, the correlation of root pressure with hydathode secretion suggests the functional significance of the fern hydathode is to be sought in its relationship with root pressure.

This project was initiated while I was enrolled in the Harvard course Biology 247, which included a field trip to Mexico. I would like to thank the instructors, Rolla and Alice Tryon, for organizing the trip, which was financially supported by the Atkins Fund of Harvard University. I also thank the Tryons for advice during early phases of the project and P. B. Tomlinson and M. H. Zimmerman for their critical review of the manuscript. Frank Lang provided the photograph in *Figure 1; Figure 2* was photographed with the assistance of George Wilder.

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A Reclassification of the Fern Genus Pyrrosia[1]

K. H. SHING*

The name *Pyrrosia,* although published by Mirbel in 1803, was overlooked by pteridologists until relatively recently. Instead, the synonyms *Cyclophorus* Desv., 1811, or *Niphobolus* Kaulf., 1824, were used. Giesenhagen (1901) published the only monograph, treating 50 species in *Niphobolus* and describing their venation, epidermis, and indument. Farwell (1931, pp. 241–246) recognized that *Pyrrosia* is the correct name of the genus. R. C. Ching (1935) studied the species of the Asian mainland, Japan, and Taiwan Province of China. He transferred 49 known species to *Pyrrosia* and described five new species. This has been the only extensive systematic paper on the genus. Nayar and others (1961, 1965, 1967) did detailed work on the morphology and anatomy of the Indian species of *Pyrrosia* in which they divided the 13 Indian species into six groups, some of which are apparently unnatural and inconvenient to use. For example, they placed *P. lingua* (Thunb.) Farw., which has stellate hairs with only lanceolate arms in the *P. heteractis* group, although each stellate hair of *P. heteractis* (Mett. ex Kuhn) Ching has 1–3 longer, acicular arms in addition to the lanceolate arms. Van Alderwerelt van Rosenburg (1908, pp. 678–696) divided 34 Malesian species into two sections under the generic name *Cyclophorus.* Section *Niphobolus* had venation similar to that of *Campyloneurum* (more or less regular, subquadrangular areolae with two or more simple or forked, included, extrorse veinlets). Section *Niphopsis* had venation similar to that of *Pleopeltis* (more or less irregularly netted with single, free, included, variously oriented veinlets). This arrangement has something to recommend it, but since the blade of *Pyrrosia* is very thick and in most species the veins cannot be seen without clearing, venation is difficult to use for identifications.

In China, *Pyrrosia* is an herb of traditional use. Since the laminae are shaped like a dagger with a leathery texture and usually trail on rocks, it was called "Rocky Leather" or "Flying Dagger" in old Chinese herbals. It is a diuretic which can be used to clean the lungs and to alleviate fever. Now in the pharmacy there are two kinds of medicine on the market, "Shiwei Tablet" and "Instant Shiwei Powder" (Shiwei in Chinese means *Pyrrosia),* made from *Pyrrosia* plants and said to have curative effects for nephritis and chronic tracheitis. Since special care is unnecessary for the survival of these plants, except for good drainage, they may be cultivated in pots, on tree trunks, on rocks, or even on the ground. The evergreen fronds with many sori covered with white or light brown, stellate hairs give them a nice appearance, and plants have been introduced into many countries for use in gardens or homes as ornamental plants. As commercial ferns, they compare favorably with Boston Fern *(Nephrolepis)* or Goldback Fern *(Pityrogramma).* In the last few years,

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[1] This work was finished in Beijing, China, but during the writer's visit to the United States, he received a grant from the National Science Foundation (020158) and through the kindness of the curators had the opportunity to examine more specimens in the following herbaria: GH, MICH, NY, and US. He would like to extend his thanks to Prof. R. C. Ching and Prof. W. H. Wagner, Jr. for their kind guidance, to Mr. M. G. Price for his helpful discussions, and to Dr. A. F. Tryon for her helpful discussion of spore characters and for providing SEM photograph for *Figure 2.*

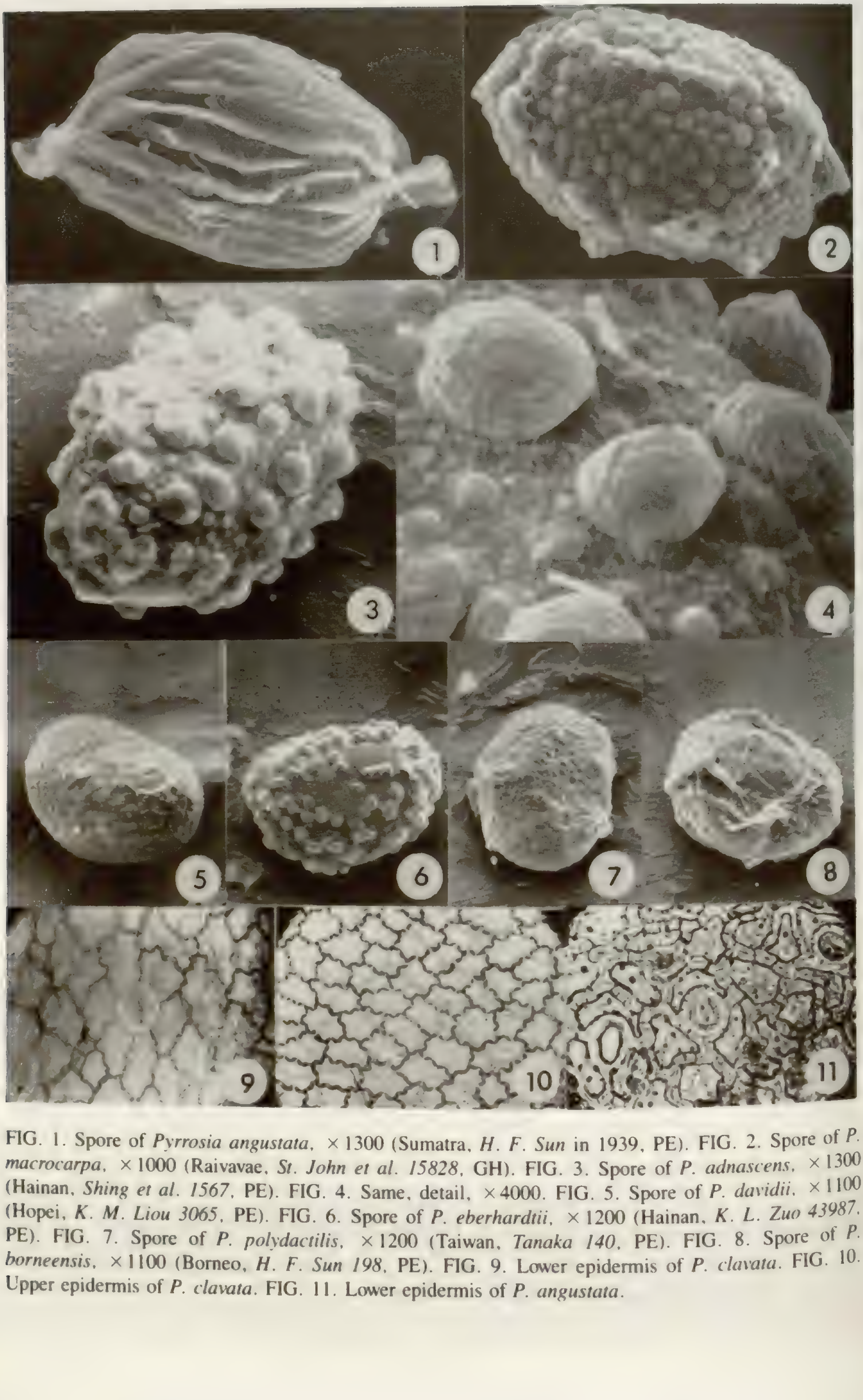

FIG. 1. Spore of *Pyrrosia angustata*, ×1300 (Sumatra, *H. F. Sun* in 1939, PE). FIG. 2. Spore of *P. macrocarpa*, ×1000 (Raivavae, *St. John et al. 15828*, GH). FIG. 3. Spore of *P. adnascens*, ×1300 (Hainan, *Shing et al. 1567*, PE). FIG. 4. Same, detail, ×4000. FIG. 5. Spore of *P. davidii*, ×1100 (Hopei, *K. M. Liou 3065*, PE). FIG. 6. Spore of *P. eberhardtii*, ×1200 (Hainan, *K. L. Zuo 43987*, PE). FIG. 7. Spore of *P. polydactilis*, ×1200 (Taiwan, *Tanaka 140*, PE). FIG. 8. Spore of *P. borneensis*, ×1100 (Borneo, *H. F. Sun 198*, PE). FIG. 9. Lower epidermis of *P. clavata*. FIG. 10. Upper epidermis of *P. clavata*. FIG. 11. Lower epidermis of *P. angustata*.

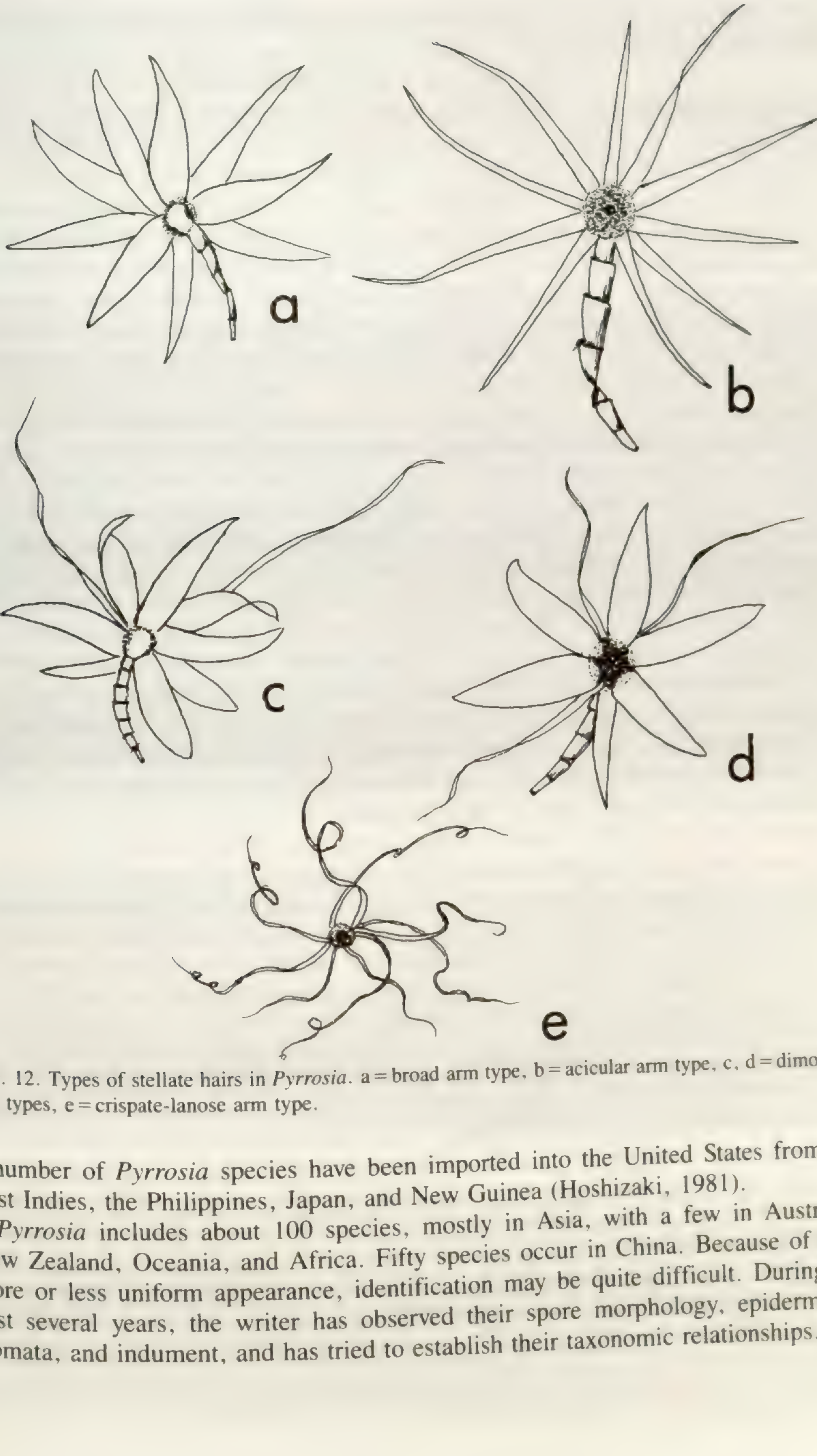

FIG. 12. Types of stellate hairs in *Pyrrosia*. a = broad arm type, b = acicular arm type, c, d = dimorphic arm types, e = crispate-lanose arm type.

a number of *Pyrrosia* species have been imported into the United States from the East Indies, the Philippines, Japan, and New Guinea (Hoshizaki, 1981).

Pyrrosia includes about 100 species, mostly in Asia, with a few in Australia, New Zealand, Oceania, and Africa. Fifty species occur in China. Because of their more or less uniform appearance, identification may be quite difficult. During the past several years, the writer has observed their spore morphology, epidermises, stomata, and indument, and has tried to establish their taxonomic relationships. The

present paper will discuss these characters and will propose a new classification scheme for the genus.

MORPHOLOGICAL CHARACTERISTICS

Spores.—Almost all species of the genus have a uniform, tubercular perine, which varies only slightly in size and thickness *(Figs. 2–8)*. However, spore ornamentation of *P. angustata* (Swartz) Ching is sharply different from most other members of the genus, and appears ribbed under the SEM *(Fig. 1)*. Since the fronds are dimorphic and firmly coriaceous, the sori very large, round, deeply sunk, and uniseriate on each side of the costa, J. Smith (1857, p. 6) considered this species to be a separate genus, *Niphopsis*. But in my opinion, considering all important features, it is really a member of *Pyrrosia*. Another similar species, *P. samarensis* (Mett. ex Presl) Ching, has the same spore ornamentation. I propose to use the rank of subgenus to indicate their advanced position in *Pyrrosia*.

Rhizome scales.—The rhizome scales of *Pyrrosia* are either entire or are ciliolate with the hairs spread along the sides or sometimes with a tuft of hairs at the apex. Since the scales are easily broken and their tips lost on most specimens, it is difficult to use this feature for identification. However, since the scales of different species may also be very different in form, size, and texture, they still are useful for distinguishing some species.

Epidermis and stomata.—The arrangement of the upper epidermal cells in the genus is uniform *(Fig. 10)*. There are, however, mainly two types of stomata in the lower epidermis. Most are pericytic, with the stomata completely surrounded by a single subsidiary cell with guard cells and subsidiary cell not linked together by any anticlinal walls *(Figs. 9* and *11)*. Some are polycytic, having the stomata in large part surrounded by a single, U-shaped subsidiary cell with the anticlinal cell walls of the guard cells and the subsidiary cell linked together toward the distal end. A few are desmocytic or copericytic (Sen & Hennipman, 1981).

Indument.—There are four kinds of stellate hairs in different groups of *Pyrrosia:* the broad arm type has 6–9 lanceolate arms *(Fig. 12*, a), the acicular arm type has 8–12 acicular arms *(Fig. 12*, b), the dimorphic arm type has 6–9 lanceolate arms and 1–3 acicular arms *(Figs. 12*, c and d), and the crispate-lanose arm type has the arms crisped and intertwined like cotton velvet, mostly on the bottom layer of the dense, thick indument (*Fig. 12*, e). Hair types are a constant and reliable character for subdividing the genus.

CONSPECTUS OF THE GENUS PYRROSIA

Pyrrosia subg. Pyrrosia

TYPE: *Acrostichum lingua* Thunb. [=*Pyrrosia lingua* (Thunb.) Farw.].

Pyrrosia sect. Pyrrosia

TYPE: *Acrostichum lingua* Thunb. [=*Pyrrosia lingua* (Thunb.) Farw.].

Pyrrosia ser. Pyrrosia

TYPE: *Acrostichum lingua* Thunb. [=*Pyrrosia lingua* (Thunb.) Farw.].

This is the largest series in the genus, with nearly 40 species, and is widespread in the Asian tropics and subtropics. Two species occur in Australia and one in Africa.

Pyrrosia ser. Heteractides Ching & Shing, ser. nov.

Pilis stellatis e brachiis lanceolatis necnon setis paucioribus (1–3) aciculatibus longioribusque compositis.

TYPE: *Polypodium heteractis* Mett. ex Kuhn [=*Pyrrosia heteractis* (Mett. ex Kuhn) Ching].

This series includes only *P. heteractis*, which is found in southwestern China, Vietnam, and the Himalayan area, and *P. eberhardtii* (Christ) Ching, distributed in southern China and Vietnam.

Pyrrosia ser. Drakeanae Ching & Shing, ser. nov.

Pilis stellatis e brachiis 8–12 aciculatis compositis.

TYPE: *Polypodium drakeanum* Franch. [=*Pyrrosia drakeana* (Franch.) Ching].

This series includes about 20 species from eastern Asia to southeastern Asia, with one species in Africa.

Pyrrosia sect. Dichlamys Ching & Shing, sect. nov.

Frons subtus indumento bistrato e pilis stellatis stipitatis dimorphis laxe composito praedita, superne e pilis aciformibus, et inferne e pilis lanosis crispatis compositis.

TYPE: *Niphobolus mollis* Kunze [=*Pyrrosia mollis* (Kunze) Ching].

Pyrrosia ser. Costatae Ching & Shing, ser. nov.

Pilis strati superi e brachiis lanceolatis, inferi e filamentis lanosis crispatisque compositis.

TYPE: *Apalophlebia costata* Presl [=*Pyrrosia costata* (Presl) Tag. & Iwats.].

This series includes, besides the type species, *P. nummularifolia* (Swartz) Ching and *P. strigosa* (Swartz) Ching; the species are limited to the Himalayas and southeastern Asia.

Pyrrosia ser. Molles Ching & Shing, ser. nov.

Pilis strati superi e brachiis longe aciculatis compositis, inferi crispatis lanosisque.

TYPE: *Niphobolus mollis* Kunze [=*Pyrrosia mollis* (Kunze) Ching].

This series contains more than 20 species, with one in Africa.

Pyrrosia subg. Niphopsis (J. Smith) Shing, comb. & stat. nov.

Niphopsis J. Smith, Cat. Cult. Ferns 6. 1857. TYPE: *Polypodium angustatum* Swartz [=*Pyrrosia angustata* (Swartz) Ching].

Rhizome thick, long-creeping, the scales caudate-lanceolate, grayish brown toward the apex and broken off in age, dark brown toward the persistent base; leaves fully dimorphic, the sterile blades shorter, lanceolate or elliptic-lanceolate, the fertile blades longer, linear-lanceolate or often narrowed to a linear apex; sori large, round or oblong, in a single series along the costae; spores bilateral, with many linear ridges, contracted at each end to an abrupt beak.

This subgenus includes two species distributed in southeastern Asia, Singapore, Malaya, Indonesia, and the Philippines to New Guinea and New Zealand. Morphologically this subgenus is advanced in the genus. Its perispore is similar to that of some species of *Dryopteris*. *Pyrrosia samarensis* (Mett. ex Presl) Ching has the same spore ornamentation as *P. angustata*, but its sterile leaf is narrower and its sori are confluent at maturity. Its laminae bear many, dark brown, stellate hairs with aciculate arms covering the hairs of the basal layer of indument, which are of the crispate-lanose type. This species is endemic to the Philippines.

NEW COMBINATIONS IN PYRROSIA

According to my studies, the following species require names in *Pyrrosia:*

Pyrrosia dispar (Christ) Shing, comb. nov.
Cyclophorus dispar Christ, Nova Guinea 8:155. 1909.—New Guinea.

Pyrrosia intermedia (Goy) Shing, comb. nov.
Cyclophorus intermedia Goy, Queensl. Nat. 10:48, t. 6. 1937.—Queensland.

Pyrrosia macrocarpa (Copel.) Shing, comb. nov.
Cyclophorus macrocarpa Copel. Univ. Calif. Publ. Bot. 12:381. 1931.—Pacific Islands.

This species is somewhat similar to *P. angustata* in outline, and Christensen (Ind. Fil. Suppl. 3:65. 1934) reduced it to a variety. It differs from *P. angustata* in that the plants are smaller, the spore ornamentation is closely tubercular *(Fig. 2),* and the sori are never impressed. It is found only in several islands of the Pacific, such as the Cook Islands, Pitcairn Island, and the Austral Islands.

Pyrrosia distichocarpa (Mett.) Shing, comb. nov.
Polypodium distichocarpum Mett. Ann. Lugd. Bat. 2:231. 1866.—Sumatra.
Cyclophorus winckleri Rosenst. Repert. Sp. Nov. Fedde 7:149. 1909.—Sumatra.
Pyrrosia winckleri (Rosenst.) Tagawa, Acta Phytotax Geobot. 25:180. 1973.

Pyrrosia winckleri and *P. distichocarpa* are here united for the first time. I have seen several specimens of the latter species, but no type material.

Pyrrosia borneensis (Copel.) Shing, comb. nov.
Cyclophorus borneensis Copel. Phil. J. Sci. 12C:64. 1917.—Borneo.

Pyrrosia rasamalae (Racib.) Shing, comb. nov.
Polypodium rasamalae Racib. Pterid. Buit. 99. 1899.—Java.

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Notes on the Ecology and Development of Plagiogyria fialhoi

PAULO G. WINDISCH* and MARILIA PEREIRA-NORONHA**

Plagiogyria fialhoi (Fée & Glaziou) Copel. is a shade-loving fern that can be found in cloud forests of elevated regions in the Brazilian states of Rio de Janeiro, Espirito Santo, Minas Gerais, São Paulo, Santa Catarina, Rio Grande do Sul, and probably also Paraná (Brade, 1956; Sehnem, 1967). Some authors (e.g., Tryon & Tryon, 1982) consider *Plagiogyria* in America to be a single species, *P. semicordata* (Presl) Christ, but in this study the separation into six species by Lellinger (1971) was adopted.

Some aspects of the ecology and development of the gametophytes and sporophytes of a population of *P. fialhoi* occurring in a cloud forest in the Serra da Mantiqueira in southeastern Brazil (45°25′S, 22°40′W, ca. 2,000 m alt.) were studied. The locality is on a small ridge next to the Campos do Jordão State Park, in the state of São Paulo. Cloud forests occur mainly on the eastern slopes of the mountains, above 1,600 and up to 2,000 m alt., and are composed of low (ca. 6 m) trees covered by a great quantity of epiphytes. Frequent drizzle, fog, and low clouds keep the humidity extremely high. The rainfall at the locality is thought to be about 2,000 mm per year.

Climatological data collected at considerably lower altitudes in the nearby state park (Seibert et al., 1975) indicate July as the driest month (ca. 30 mm rainfall) and January as the wettest (more than 300 mm). The warmest month is February (17.7°C average, absolute maximum 27.2°C); the coldest is July (9.5°C average, absolute minimum −4.4°C). A short description of the floristic composition of these cloud forests is presented by Seibert et al. (1975), together with the detailed climatic data for the region.

MATERIALS AND METHODS

Gametophytes and ca. 60 young sporophytes with fronds up to 3 cm long were collected and preserved in weak chromo-acetic fixative (Sass, 1951); 36 larger specimens were pressed (voucher specimens at HRCB). Frond longevity was studied in 15 plants by marking their youngest fronds and following their development during visits 240 and 374 days later (February and June, 1982). The complete underground parts (rhizome, roots, and stipe bases) of ten well developed specimens were carefully removed and the shape and position of the rhizome correlated with the topography.

The average number of fronds per adult plant was calculated from data from the ten removed specimens (April, 1981) and from the 15 marked plants (June, 1981). Average size of the fronds was obtained based on those of the 10 removed specimens and confirmed later (March, 1983) by measuring 128 adult fronds. The distance between the elements of 55 pairs (nearest neighbors) of plants was measured.

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FIGS. 1–14. Gametophytes and heteroblastic development of the sporophyte of *Plagiogyria fialhoi*. FIGS. 1–4. Gametophytes attached to young sporophytes. FIGS. 5–12. Sporophytes in diverse stages of development. FIG. 13. Lamina of a frond 15.5 cm long. FIG. 14. Pinna from the middle of a frond 40 cm long.

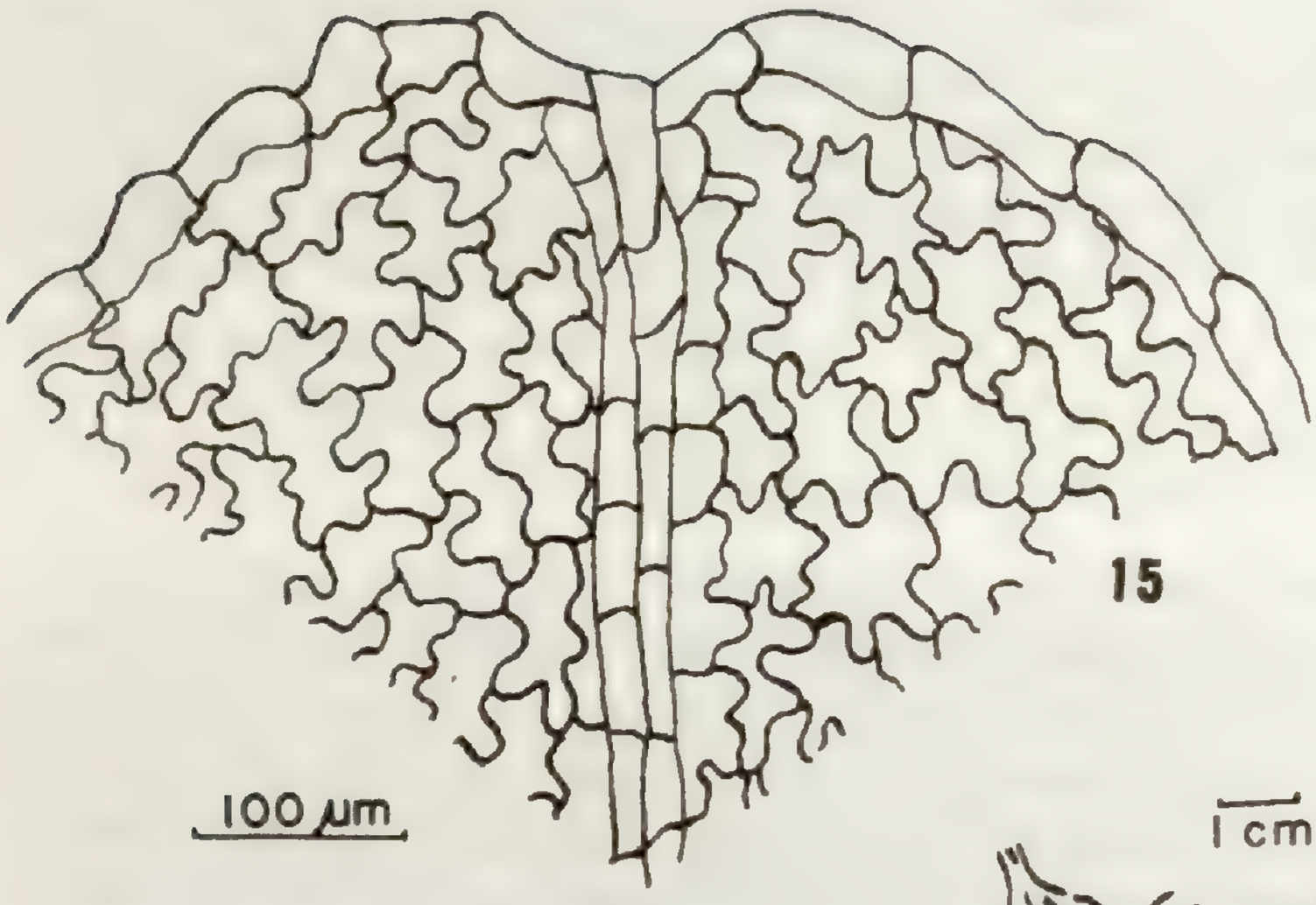
Humus and soil samples were taken from ten points (March, 1983), keeping the top material (0–5 cm depth) separated from the humus-soil mixture below (5–10 cm depth). Spores were collected (June, 1981 and February, 1982) and germinated in the laboratory after storage at 3–5°C for three and 120 days, using a solid agar medium (technique described by Dyer, 1979). Gametophyte cultures were kept for 100 days growing under 850 lux (fluorescent plus incandescent bulbs, 12 hours/day) at ca. 24°C.

RESULTS AND DISCUSSION

Plants of *P. fialhoi* were found in great numbers on the steep, humid slopes (30–50% declivity) of the southeastern side of the ridge, which rises ca. 70 m above a small stream. The density of plants increases closer to the water. The distance (nearest neighbor) between the elements of 21 pairs of plants growing more than ca. 10 m from the stream was 45–520 (ave. 189.4) cm, whereas the distance between the elements of 34 pairs growing within 10 m of the stream was 18–300 (ave. 95.9) cm. The plants grew in the rich humus layer that covers the ground. Humus samples from the top layer (5 cm) had a pH of 3.2 (in $CaCl_2$); 48μg/cm^3 P (resin method) and K, Ca, Mg, H + Al values (m. eq. 100 cm^3) of 0.5, 0.8, 0.6, and 24.4. Samples from the humus and soil mixture (19.6% organic matter) from the layer below (5-10 cm) had a pH of 3.1; 43 μg/cm^3 P; and K, Ca, Mg, H + Al values of 0.29, 0.2, 0.3, and 46.0, respectively.

In a few places on the slope, associations of gametophytes and juvenile sporophytes of *Plagiogyria* in diverse stages of heteroblastic development, together with fern gametophytes and young sporophytes of other species, mosses, liverworts, and angiosperm seedlings were found. In contrast with the surrounding area, where the adult fern sporophytes occurred, the amount of organic matter on the ground at those spots was very small, indicating that these associations were of a pioneer nature, probably covering soil exposed by running water or fallen trees.

In nature, the first frond of the young sporophytes (still attached to the gametophytes) measured 5.5–8.0 (ave. 7.0) mm long, with stipes 3.0–5.2 (ave. 3.9) mm long and laminae 1.3–4.3 (ave. 3.1) mm long. These laminae were symmetric and bilobed or asymmetric with one of the segments once more lobed (*Figs. 1–5*). The margin of the laminae in plants of all developmental stages presented a characteristic row of more or less rectangular cells (*Fig. 15*), which was of basic importance in the identification of juvenile specimens. Fronds ca. 14–35 mm long had a central vascular strand and tended to form pinnatifid laminae (*Figs. 6–7*). Pinnatisect to pinnate laminae were observed on plants with fronds longer than 35 mm (*Figs. 8–13*). These fronds (up to 80 mm long) had segments with serrate margins and simple veins. The lower pinnae of fronds ca. 85–150 mm long had biserrate margins (*Fig. 13*) and bifurcate proximal veins. Free veins that reach the lamina margins was a consistent character in all stages of development. The sterile laminae of adult sporophytes had biserrate margins (*Fig. 14*), and most of the veins were bifurcate, so that a veinlet ended in each tooth. In well developed specimens (with rhizomes longer than 6 cm) the fronds were 43–117 (ave. 75.68) cm long, the stipe representing about 1/3 of the total length.



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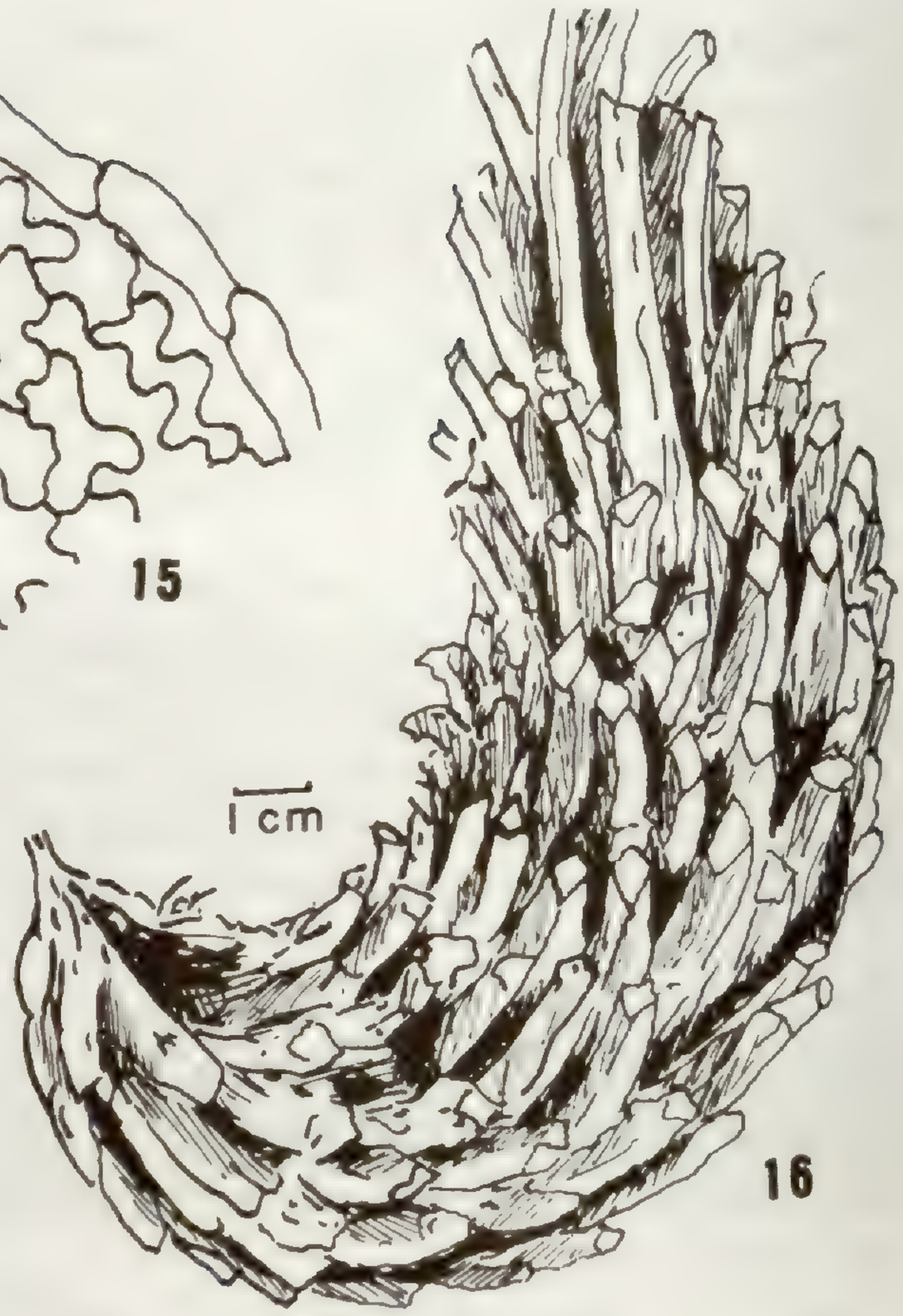

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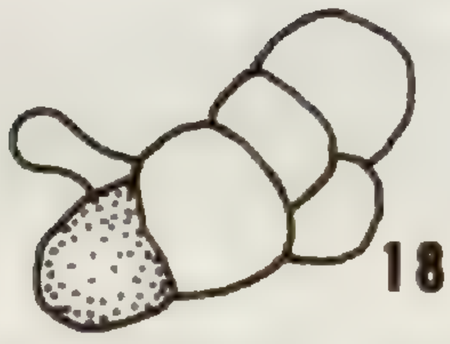

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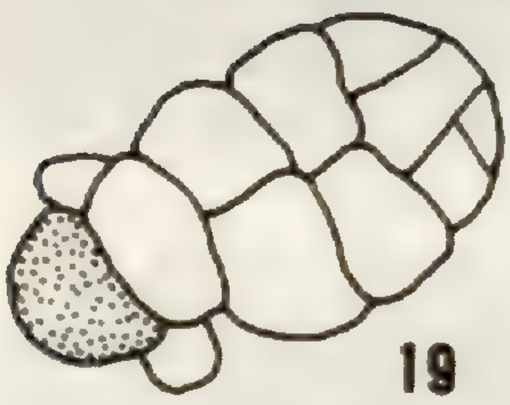

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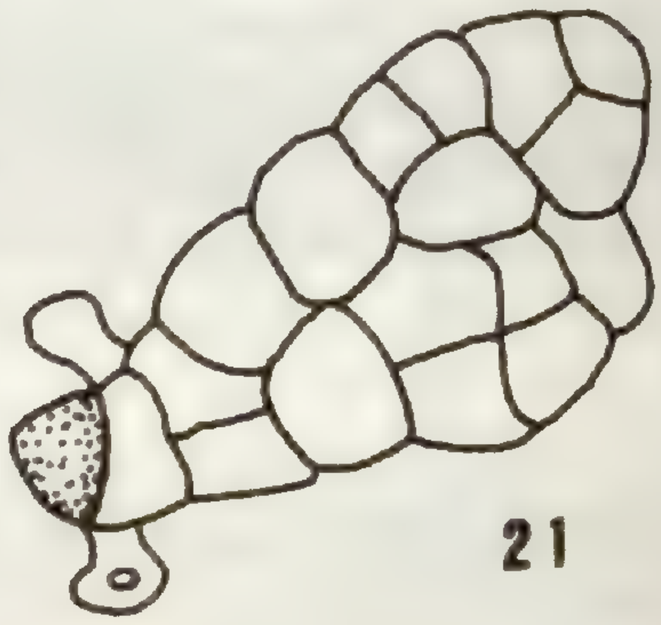

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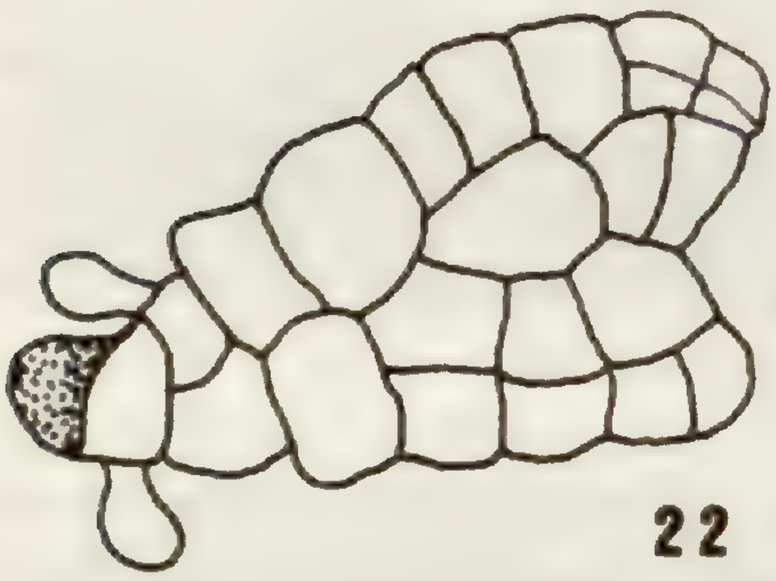

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FIGS. 15–23. Detail of the lamina and rhizome of the sporophyte and early stages of gametophyte development of *Plagiogyria fialhoi*. FIG. 15. Laminar margin of a young sporophyte. FIG. 16. Adult, curved rhizome (old stipe bases removed). FIGS. 17–23. Early developmental stages of gametophytes grown in the laboratory.

Fertile fronds were observed from February to June. It seems that they are formed around January and probably persist until July. Viable spores were collected in June, 1981. A visit in February, 1982 revealed many young fronds, but the spores collected from the most developed of these did not germinate. These data indicate a definite periodicity of fertility. Fertile fronds measured 70–117.5 (ave. 103.0) cm long (the stipe representing about 1/2 of the total length) and were usually longer than the sterile fronds of a given plant. The minimum ratio observed for numbers of sterile to fertile fronds observed was 10:4, the maximum 21:1.

The rhizome, covered with the bases of fallen fronds and adventitious roots, was usually erect if no longer than 4 cm, but curved in larger specimens so that the vegetative parts usually were level with or barely above the litter on the ground. The older parts remained buried. The apex of each rhizome bore the fronds in a rosette protecting frond primordia and young fronds. Litter carried down the slope accumulated against the frond-covered rhizome apices. The resulting pressure on the uphill side and perhaps a more intense washing of the ground on the other side, together with apical rhizome growth, promoted a slow and gradual movement of the whole plant downhill. The rhizome and its semi-decayed remains are curved, with the main axis oriented down the slope. In a large specimen, the angle of deviation between the alignment of the rhizome apex and that of the oldest remains was ca. 155° (*Fig. 16*), indicating the change of relative position of the old parts in the ground due to the downhill movement.

The one year-long observation of marked fronds revealed that fronds persisted for about one year. The number of fronds on adult plants (of different ages) was 9–21 (ave. 12). Therefore, the minimum age of a plant can be estimated by dividing the total number of stipe bases by 12. On very old specimens, the semi-decayed parts still present are of large size, indicating that at the time those were formed the plant was already well developed. One specimen with a rhizome 21 cm long had a minimum age of 24 years. The youngest fertile specimen collected had a rhizome 12 cm long; its age was estimated to be more than 15 years, indicating a minimum spore-to-spore life cycle of considerable duration. Vegetative reproduction was not observed, although Bower (1926) cited the occurrence of stolons in *P. pycnophylla* (Kunze) Mett. and bifurcation of the rhizome in *P. semicordata*.

Spores sown on culture media three days after collection did not germinate up to 30 days after sowing, but after 50 days, germinating spores and gametophytes with 3, 4, 9 and 12 cells were seen. Slow germination occurring at irregular intervals was also observed in cultures of *P. glauca* (Blume) Mett. and *P. semicordata* by Stokey and Atkinson (1956). This kind of gradative germination can explain the finding in nature of gametophytes together with young sporophytes in diverse stages of development in a single small area. Spores stored for 120 days showed an extremely low germination rate; a single spore in about 2,000 germinated after 30 days, reconfirming the short viability of the spores of this genus as discussed by Stokey and Atkinson (1956) and Nayar and Kazmi (1962).

The first stages of gametophyte development (*Figs. 17–20*) are very similar to those described by Nayar and Kazmi (1962) for *P. triquetra* Mett. No apical meristematic cell was observed. The development of a heart-shaped apex (*Figs.*

21–23) started earlier (65 days after sowing) than in the Old World species studied by Nayar and Kazmi (1962). Elongated young plate stages and filamentous stages as cited for *P. glauca* and *P. semicordata* by Stokey and Atkinson (1956) were not observed; perhaps they were a consequence of the physical conditions under which Stokey and Atkinson's material was grown. They considered the probability of competition with algae as being the cause of these elongated plate stages, but our cultures were also heavily contaminated. Unfortunately, the algae were so numerous that further development of the gametophytes could not be followed in the laboratory. In nature, we found that mature gametophytes were cordiform (up to 4.4 mm wide, 5.3 mm long at the larger wing), generally with one of the wings overlapping the other (*Figs. 1–4*), and had a thick central region.

This study was made possible by the cooperation of the officers of the Forestry Institute of the State of São Paulo, Campos do Jordão State Park and by support from the Conselho Nacional de Desenvolvimento Científico e Tecnológico—CNPq (Proc. 30.1339/77 and Proc. 10.6254/79), the Universidade Estadual Paulista Júlio de Mesquita Filho—UNESP, and the Fundação de Amparo à Pesquisa do Estado de São Paulo—FAPESP (Proc. 81/1369-5).

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The Ferns of Elden Mountain, Arizona

MICHAEL D. WINDHAM*

Elden Mountain, located immediately northeast of Flagstaff in north-central Arizona, is an unusual volcanic peak with a diverse fern flora. The earliest pteridophyte collections from the area are those taken by L. N. Goodding in 1913. Whiting and Bradey collected extensively on the mountain during the 1930's and were apparently the first to encounter *Asplenium adiantum-nigrum* in 1935. In a short article discussing the occurrence of this species in Arizona, Wherry (1941) mentioned five other ferns casually observed during a visit to the locality. Phillips (1946, 1947) listed five additional taxa for the mountain, bringing the number of reported species to 11. The flora of Elden Mountain received little attention during subsequent years, and much of the area remained unexplored when a forest fire inflicted heavy damage in June, 1976. Concerned about the fate of several rare species, I began a comprehensive survey of surviving fern populations in 1978.

Elden Mountain is a massive dacite dome located near the center of the San Francisco volcanic field. Although precise dates are not yet available, geologists agree that the dome was formed sometime during the last million years (Kluth & Kluth, 1974). The dacitic magma was quite viscous, and well-defined lava flows are evident on all slopes. Juxtaposition of lava flows created a highly complex topography, and erosion has produced innumerable cracks and crevices that provide favorable habitats for a variety of unusual plants. The elevation at the base of the mountain averages 7000 feet; the summit falls just short of 9300 feet.

A lengthy meteorological record is available for nearby Flagstaff at 6900 feet elevation (Sellers & Hill, 1974); much of the general climatic data is applicable to Elden Mountain. At Flagstaff, the lowest average monthly temperature (27.3° F) occurs in January, the highest (65.5° F) in July. The mean frost-free period extends from June 8 to September 26, a total of 110 days. Annual precipitation averages 18.31 inches, and seasonal rainfall patterns are distinctly bimodal. The greatest amount of rainfall occurs in July and August, when storm systems enter the region from the Gulf of Mexico. Pacific-based storms produce a second precipitation peak in January and February, but the months of May, June, and November are characterized by drought, which was a major factor in the disastrous fire of 1976.

The distinct vegetation zones observed on the San Francisco Peaks (Merriam, 1890) are all but absent on Elden Mountain. Abrupt topography brings diverse habitats into close proximity, and plant associations on the peak are extremely complex. The areas surrounding the base of the mountain are dominated by *Pinus ponderosa*, which is frequently associated with *Quercus gambelii*. South-facing slopes exhibit a dense cover of *Cercocarpus montanus*, *Berberis fremontii*, *Juniperus deppeana*, *J. osteosperma*, *Pinus edulis*, *Opuntia phaeacantha*, and *Yucca baccata*. The northern slope and crest of the mountain support a mixed conifer forest in which *Pseudotsuga menziesii*, *Abies concolor*, and *Pinus flexilis* dominate. Small meadows and stands of *Populus tremuloides* occupy a limited area near the summit. Some areas show a haphazard mixture of all the species mentioned above.

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METHODS AND MATERIALS

The data presented herein result from intensive fieldwork undertaken between February, 1978 and March, 1983. Considering the size and complexity of Elden Mountain, it would be unwise to suggest that the pteridological survey is complete. However, most suitable habitats have been examined, and recent visits to the area have failed to yield additional, unreported species. Detailed field notes were kept concerning the distribution and habitat preference of each taxon, and population estimates were derived through a census of individual adult plants. Ten mature sporangia were gathered from each species, and their contents were examined in glycerol to determine spore number. Most cytological materials were field fixed in May and June using Farmer's solution (3 parts ethanol: 1 part glacial acetic acid). Plants not demonstrating the proper meiotic condition were transferred to a greenhouse to stimulate the production of fertile fronds. Fixed sporangia were hydrolyzed for approximately 15 minutes in 1N HCl prior to staining with aceto-orcein. Hoyer's solution was used as the squashing and mounting medium in all chromosome preparations. Counts were derived from cells at late diplotene or diakinesis and were documented using a camera lucida. Voucher specimens for all phases of this study have been deposited at the Deaver Herbarium, Northern Arizona University (ASC).

RESULTS AND DISCUSSION

All fern species previously reported for Elden Mountain were relocated during this survey, proving that none was lost as a direct result of the 1976 fire. In fact, the number of recognized species was nearly doubled by the discovery of two unreported herbarium collections and seven taxa new to the mountain. None of the additions were found in fire-damaged areas, and it is apparent that they have existed on the mountain for quite some time. Nearly all are characterized by low population densities, which may explain why they were overlooked by previous collectors. The survey has revealed that the Elden Mountain fern flora comprises 20 species representing 11 genera. Chromosome counts have been obtained for 15, and spore count data are available for all but one.

Adiantum pedatum L.—Discovered in 1979, the colony consists of ca. 25 plants growing on the western slope at 8100 ft elevation. The plants are confined to a small area of permanent seepage on the back wall of a narrow cliff recess. The length/width ratio of the laminae is unusually high compared to other Arizona collections, but elongate fronds are occasionally observed throughout the range of the species. Mature sporangia consistently produced 64 normally developed spores.

Asplenium adiantum-nigrum L.—The Elden Mountain population comprises at least 100 individuals scattered over the southern and eastern slopes at 7100–8100 ft elevation. The plants favor shaded cracks, crevices, and ledges on relatively dry, south-facing cliffs. All sampled sporangia yielded 64 normal spores, and a chromosome count of $n = 72$ II (*Fig. 1A*) agrees with previous determinations from Europe and Colorado (Shivas, 1969) Colorado specimens were originally described as *Asplenium andrewsii* A. Nels., and Chihuahuan collections provided the type materials of *A. chihuahuense* J. G. Baker and *A. dubiosum* Davenp. (Knobloch & Correll, 1962). The proliferation of names in the New World resulted from the

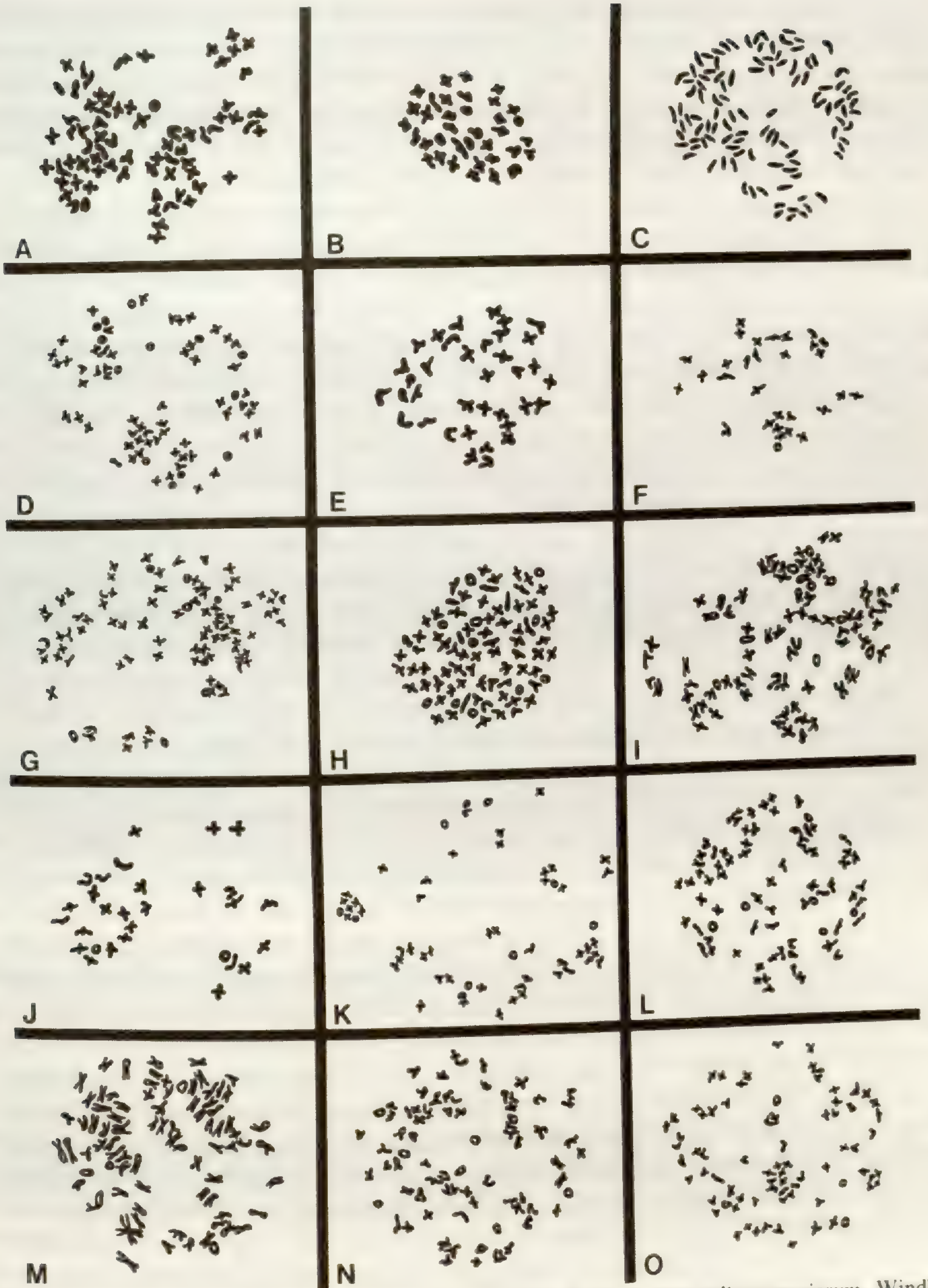

FIG. 1. Camera lucida drawings of meiotic chromosomes. A. *Asplenium adiantum-nigrum*, Windham 351. B. *A. platyneuron*, Windham 394. C. *A. resiliens*, Windham 400. D. *A. septentrionale*, Windham 393. E. *A. trichomanes*, Windham 397. F. *Cheilanthes fendleri*, Windham 26. G. *C. wootonii*, Windham & Yatskievych 266. H. *Cystopteris* cf. *tennesseensis*, Windham & Windham 319. I. *Dryopteris filix-mas*, Windham 395. J. *Pellaea truncata*, Windham 149. K. *P. wrightiana*, Windham 396. L. *Polypodium hesperium*, Windham 392. M. *Polystichum scopulinum*, Windham 398. N. *Woodsia mexicana*, Windham 402. O. *W. oregana*, Windham & Windham 253.

failure of early investigators to recognize the Eurasian affinities of these highly disjunct populations. Shivas (1969) stated that meiotic pairing in *A. onopteris* × *A. adiantum-nigrum* was identical whether the latter parent came from Europe or Colorado. A recent analysis of polyphenolic constituents (Richardson & Lorenz-Liburnau, 1982) provides further evidence that *A. andrewsii* (including all collections from Elden Mountain) is conspecific with *A. adiantum-nigrum*.

Asplenium platyneuron (L.) B.S.P.—The Elden Mountain colony is located ca. 600 km WSW of the westernmost record in Colfax County, New Mexico. My wife and I first encountered the plants in February, 1978, but there is some indication that the species was originally discovered in the 1940's. In a letter to William Maxon dated July 15, 1947 (on file at ARIZ), Dr. Phillips mentioned that an associate in California had collected an unusual *Asplenium* in northern Arizona. The precise collection locality was unknown, but Phillips tentatively identified the specimen as *A. platyneuron*. In a reply dated July 21, Maxon requested a frond from the plant in order to verify its identity. However, Maxon passed away shortly thereafter, and the species was never reported for Arizona. The local population comprises at least 150 plants on the eastern, southern, and western slopes at 7000–7600 ft elevation. For the most part, the plants are restricted to deep cracks and crevices with semi-permanent shade and an ample supply of moisture. Individuals occupying more exposed habitats tend to develop coriaceous pinnae with prominent marginal serrations. The colony appears to be actively reproducing, and all sampled sporangia contained 64 normal spores. Local plants are morphologically similar to those of the eastern United States, and a chromosome count of $n = 36$ II (*Fig. 1B*) agrees with all previous determinations (Löve, Löve & Pichi Sermolli, 1977).

Asplenium resiliens Kunze—Discovered in 1978, this species is scattered over the southern and western slopes of the mountain at 7000–7800 ft elevation. Its preferred habitat is nearly identical to that of *A. adiantum-nigrum*, but the two species were never observed growing in close proximity. A sample of ten sporangia yielded nine with 32 normal spores and one with 64 malformed, presumably aborted spores. Meiotic squashes revealed the presence of two types of cells with different chromosome complements. Sporangia following an apogamous pathway contained eight large spore mother cells that showed $n = 108$ II. This mechanism of sporogenesis, resulting in 32 viable spores, is dominant judging from the spore count data. However, occasional sporangia follow the normal sexual pathway, and they contain 16 smaller spore mother cells at the beginning of meiosis. Manton (1950) suggested that the latter cells provide evidence of genome homologies in hybrid taxa reproducing by apogamy. In the Elden Mountain collections, all cells of this type showed $n = 108$ I (*Fig. 1C*). These data confirm previous observations that the species is an apogamous triploid and suggest that the putative diploid and tetraploid parents were not closely related.

Asplenium septentrionale (L.) Hoffm.—Widely distributed on all slopes of the mountain at 7100–8700 ft elevation. The plants occupy a variety of habitats, but most are found in shaded cracks on exposed boulders and cliff faces. They appear to be morphologically indistinguishable from European specimens, and all sampled

sporangia contained 64 normal spores. A chromosome count of $n=72$ II (*Fig. 1D*) agrees with previous determinations in Eurasia (Löve, Löve & Pichi Sermolli, 1977) and the disjunct population in Monroe County, West Virginia (Emory, 1970).

Asplenium trichomanes L. subsp. trichomanes.—Found in deep cracks and crevices on all slopes of Elden Mountain at 7000–8300 ft elevation. Plants are closely associated with *A. platyneuron* in several places, but there is no evidence of local hybridization. Mature sporangia consistently produced 64 normal spores with a mean diameter of 28 μm. Moran (1982) assigned Arizona collections to the diploid cytotype on the basis of spore dimensions, and a chromosome count of $n=36$ II (*Fig. 1E*) substantiates his prediction.

Cheilanthes eatonii Baker—Discovered in 1978, this fern inhabits exposed ledges and cliffs on the southern and western slopes at 7000–8100 ft elevation. Considering its abundance on the south side of the mountain, it is surprising that the species was overlooked by previous collectors. Local materials have traditionally been assigned to forma *eatonii*, which exhibits a dense tomentum on the upper surface of the frond. All sampled sporangia yielded 32 large, well formed spores, suggesting that the plants are apogamous.

Cheilanthes feei Moore—Common on all slopes of the mountain, this species favors relatively dry, exposed cliffs at 7000–8500 ft elevation. The presence of 32 spores in each sporangium suggests that local plants are apogamous triploids similar to those studied by Knobloch (1967).

Cheilanthes fendleri Hook.—Discovered in 1978, the Elden Mountain population comprises at least 50 plants on the eastern, southern, and western slopes at 7200–8100 ft elevation. Most plants inhabit well shaded ledges on the eastern side of the mountain. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=30$ II (*Fig. 1F*) is apparently the first report for the species.

Cheilanthes wootonii Maxon—Favoring shaded ledges on south-facing cliffs, this species is scattered over the eastern, southern, and western slopes at 7100–7700 ft elevation. Mature sporangia consistently produced 32 large, well formed spores. Meiotic squashes revealed that both apogamous and sexual pathways operate during sporogenesis, although the latter was rarely observed. Sporangia following the apogamous pathway contained eight large spore mother cells that showed $n=90$ II (*Fig. 1G*). Sporangia utilizing the sexual pathway contained 16 smaller spore mother cells at the beginning of meiosis. It was not possible to obtain an exact chromosome count on cells of this type, but several preparations suggest that $n=$ ca. 30 II + 30 I. Most univalents do not converge on the plate during metaphase, and the resultant unequal distribution of chromosomes leads to spore malformation. These data indicate that local plants of *C. wootonii* are apogamous triploids of hybrid origin. A Texas plant studied by Knobloch (1967) showed $2n=116$, suggesting that this polymorphic species includes at least two cytotypes.

Cystopteris cf. tennesseensis Shaver—Not previously reported for Arizona, although a number of pteridologists have been aware of its occurrence in the state (W. H. Wagner, pers. comm., 1982). The Elden Mountain colony is located ca. 700 km NW of the westernmost station in the Guadalupe Mountains of Texas (Blasdell, 1963). The species was originally collected by L. N. Goodding in 1913 and

identified as *C. fragilis*. Goodding's collection was overlooked by Phillips (1947) and omitted from his checklist of Arizona ferns. The population consists of ca. 35 plants growing on the western slope at 8000–8100 ft elevation. The plants are confined to seepage zones in deep crevices and cliff recesses; several grow in close proximity to the *Adiantum pedatum* colony. A sample of 20 sporangia was removed from two different plants, and 19 of them contained 64 normal spores. The remaining sporangium yielded 32 exceptionally large, well formed spores. Further study will be necessary to determine the viability and ploidy level of these unreduced products of sporogenesis. Chromosome counts of $n=84$ II (*Fig. 1H*) were obtained from sporangia with the normal complement of 16 spore mother cells. The presence of minute bulblets on some plants suggests that the species is an allotetraploid whose parentage includes *C. bulbifera*. The plants resemble typical *C. tennesseensis* in many respects, but the two taxa are probably not identical.

Dryopteris filix-mas (L.) Schott— This conspicuous fern is frequently collected and occurs on all slopes at 7100–8600 ft elevation. Its preferred habitat consists of shaded cracks and crevices with an ample supply of moisture. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=82$ II (*Fig. 1I*) agrees with an earlier report from western North America (Reisender, 1974). The morphology of local specimens is highly variable, and fronds range from early deciduous to evergreen.

Pellaea truncata Goodding—Discovered in 1979, the Elden Mountain colony consists of ca. 10 plants growing on the eastern and southern slopes at 7400–7700 ft elevation. The species is rarely collected on elevated sections of the Colorado Plateau, and plants are confined to dry, south-facing cliffs and ledges. A sample of ten sporangia yielded nine with 64 spores and one with 32 exceptionally large spores that may be unreduced products of sporogenesis. A chromosome count of $n=29$ II (*Fig. 1J*) agrees with previous reports (as *P. longimucronata*) by Knobloch and Britton (1963). Most fronds tend to be tripinnate at the base, but local specimens are otherwise similar to their low elevation counterparts.

Pellaea wrightiana Hook.—Common on the eastern, southern, and western slopes of the mountain at 7000–8100 ft elevation. The habitat requirements of this species are nearly identical to those of *Cheilanthes eatonii*, and the two often grow together on the low cliffs of the southern slope. A sample of ten sporangia yielded nine with 64 spores and one with 32 exceptionally large spores. This situation is not unusual in *P. wrightiana*, and all Arizona collections thus far examined have produced similar ratios. A chromosome count of $n=58$ II (*Fig. 1K*) provides further support for Wagner's (1965) assertion that this taxon is typically a fertile tetraploid. Sterile triploid hybrids between this and the preceding species have been found on the southern slope at 7100 ft elevation.

Pityrogramma triangularis (Kaulf.) Maxon—Discovered in 1979, the Elden Mountain colony provides the first record for Coconino County and indicates that the species has a much greater elevation range than was previously suspected. The colony consists of three small plants growing from a permanently shaded crack on the southern slope at 7125 ft elevation. Mature sporangia consistently produced 64

normally-developed spores. Atypical morphology and a paucity of material preclude identification at the varietal level.

Polypodium hesperium Maxon—Found in shaded cracks and crevices on all slopes of the mountain at 7600–8700 ft elevation. All sample sporangia yielded 64 normal spores, and a chromosome count of $n=74$ II (*Fig. 1L*) agrees with previous Arizona reports by Knobloch (1962) and Lloyd (1963). Local plants have acrid, pruinose rhizomes that distinguish them from typical populations in the Pacific Northwest.

Polystichum scopulinum (D. C. Eaton) Maxon—Arizona lies at the southern distributional limit of this species, and most populations are small and sporadically distributed. The Elden Mountain colony is the largest in the state, including at least 250 individuals on the western, southern, and eastern slopes at 7100–8200 ft elevation. The plants favor shaded cracks and crevices on south-facing cliffs. All sampled sporangia contained 64 normal spores, and a chromosome count of $n=82$ II (*Fig. 1M*) agrees with previous determinations by Wagner (1973).

Pteridium aquilinum (L.) Kuhn var. pubescens Underw.—This widespread taxon is rarely observed on Elden Mountain and was not collected until 1979. It favors rocky soils in open coniferous forests, occurring on all slopes at 7000–7700 ft elevation. Chromosome and spore counts are not available because the population showed no evidence of sexual reproduction from 1979 to 1983.

Woodsia mexicana Fée—Common on the eastern, southern, and western slopes of the mountain at 7000–7600 ft elevation. The plants grow on partially shaded cliffs and ledges and are often associated with *Pellaea wrightiana*. All sampled sporangia yielded 64 normal spores, and chromosome counts of $n=76$ II (*Fig. 1N*) were obtained from five different plants. These counts conflict with Knobloch and Correll's (1962) report of $n=82$ and substantiate Brown's (1964) hypothesis that the species is a tetraploid based on $x=38$. Specimens from northern Arizona and New Mexico are somewhat atypical, showing substantial reductions in the length of both indusial filaments and marginal processes.

Woodsia oregana D. C. Eaton—All Elden Mountain collections of this species have previously been referred to *W. plummerae* (Phillips, 1947). The specimens are unusually glandular and their indusial segments tend to be united at the base. However, they bear little resemblance to typical *W. plummerae* of southern Arizona, and preliminary flavonoid data indicate that the two are biochemically distinct. Scanning electron microscopy has also revealed clear and consistent differences in spore ornamentation. Seven plants from Elden Mountain were examined cytologically, all of which yielded counts of $n=76$ II (*Fig. 1O*). Similar materials gathered from four other localities in northern Arizona also proved to be tetraploid. Overall morphology suggests a close relationship to *W. oregana*, but typical collections of that species are reportedly diploid (Brown, 1964). Additional data will be necessary to resolve the apparent discrepancy between morphology and cytology. The species is sporadically distributed on all slopes at 7000–8700 ft elevation. The plants are usually found in shaded cracks and crevices, and all sampled sporangia contained 64 normal spores. Sterile tetraploid hybrids between this and the preceding species have been found on the southern slopes of Elden Mountain at 7000 ft elevation.

The fern flora of Elden Mountain includes ca. 20% of the species known to grow in Arizona. Several are relatively common in the state, but *Asplenium adiantum-nigrum* and *A. platyneuron* are apparently confined to this locality. The number of xerophytic ferns is unusually high considering the elevation, and 40% of the taxa are rarely found north or west of Elden Mountain. Included in this category are *Asplenium resiliens, Cheilanthes eatonii, C. fendleri, C. wootonii, Pellaea wrightiana* and *Woodsia mexicana*. Four species (20%) are known or suspected apomicts, showing triploid chromosome numbers and 32 spores per sporangium. Local *Pteridium* colonies are strongly rhizomatous and they, too, form the bulk of their populations without sexual processes. Approximately 69% of the sexual species are tetraploids; the remainder are diploids. Several of the tetraploids are nothospecies of hybrid origin, including *Asplenium adiantum-nigrum, Cystopteris* cf. *tennesseensis, Pellaea wrightiana,* and *Polypodium hesperium*. In each case, one or both of the putative parents are absent from Elden Mountain and there is no evidence that the species were formed locally. However, interspecific hybridization is moderately common on the mountain, and sterile hybrids have been detected in both *Pellaea* and *Woodsia*.

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REVIEW

FERNS AND FERN–ALLIES OF MEGHALAYA STATE, INDIA, by A. K. Baishya and R. R. Rao. Scientific Publishers, Jodhpur, India. viii + 161 pp. 1982. Rs. 100.—Meghalaya State is a portion of what was formerly called Assam. It occupies more than 22,000 square kilometers and lies north of Bangladesh and south of the Himalayas in northeastern India. The topography is diverse and ranges from 100 to 1990 m in elevation. Vegetation types include evergreen and semi-evergreen forests, deciduous forests, subtropical pine forests, grasslands, and temperate forests. Terrestrial, lithophilic, and epiphytic ferns are found. The pteridophytes number 256 species in 91 genera, a rich and diverse flora. None of the genera has more than 20 species; the largest are *Selaginella* and *Asplenium*. The present volume includes keys to the families, genera, and species, synonymies, descriptions, habitat and range notes in the Flora area, an interesting introduction, a bibliography, and an index. Some of the species are illustrated with photographs or line drawings. The keys seem well constructed. The book will be of interest to all who deal with the ferns of India and the surrounding region. The book is available from United Book Traders, Opposite Police Lines, Ratanada, Jodhpur 342001, India. The U.S. price of $20.00 far exceeds the rupee price.—*D.B.L.*

Donovan S. Correll (1908–1983)

Donovan Stewart Correll was born on 13 April 1908 in Wilson, North Carolina. He grew up in Winston-Salem and attended Duke University, which awarded him an A.B. in 1934 and an A.M. in 1936. From 1939 to 1943 he did graduate study at the Botanical Museum, Harvard University. He was awarded a Ph.D. by Duke University in 1943. He joined the U.S. Navy for the balance of World War II, and then worked in the Division of Plant Exploration and Introduction, U.S. Department of Agriculture, from 1944 to 1956. He was the Chief Botanist at the Texas Research Foundation from 1956 until 1972, worked for the National Science Foundation as a program director in 1972 and 1973, and then "retired" to the Fairchild Tropical Garden, where he carried out a strenuous research program until shortly before his death on 28 Mar 1983, not long after completing his monumental "Flora of the Bahamas Archipelago." His principal works on ferns were "The Ferns and Fern Allies of Louisiana" (with Clair A. Brown), the "Ferns and Fern Allies of Texas," and "The Ferns and Fern Allies of Chihuahua" (with I. W. Knobloch). Besides the ferns, his specialties were the Orchidaceae, Solanaceae, and Palmae, and also the floras of the southwestern United States and the Bahamas. His knowledge of the floras of the New World was tremendous. He conducted field work in the United States, Mexico, Central America, the West Indies (especially the Bahamas), South America, and Hawaii. An obituary and bibliography is to be published in Brittonia. —*D.B.L.*

REVIEW

FERNS AND ALLIED PLANTS. WITH SPECIAL REFERENCE TO TROPICAL AMERICA, by Rolla M. Tryon and Alice F. Tryon. xiv + 858 pp. illustr. Habitat photography principally by Walter F. Hodge. Springer-Verlag, New York. 1982. ISBN 0-387-90672-X. $148.00—Fern specialists are blessed (some would say cursed!) with almost as many classifications from which to choose as there are pteridologists. The Tryons provide us with yet another choice. In a luxurious format designed to facilitate quick reference and comparison, they give a synonymy, a description, comments on classification, a key to the genera, and selected references for each of 29 families. Each generic treatment includes a synonymy, a description, a statement on classification, a discussion of the tropical American species, often keys, discussions of ecology, geography, spores, and chromosome numbers, additional observations (mostly interesting notes on natural history), and literature. Taxonomic opinions also have been rendered at the species rank, e.g., in *Schizaea* (p. 78), *Paesia* (p. 396), and *Dryopteris* (p. 501), usually with a reduction in species. An index to scientific names completes the work.

One of the best features of the book is the abundance of good illustrations. These include habit photographs of nearly all genera, photographic details of diagnostic features (e.g., venation, indument, and sori), silhouettes of fronds (chosen to show diversity in a genus), line drawings and pencil sketches, and SEM photographs of

spores and occasionally other characters. In addition there are dot maps showing generalized American distributions for each genus; these I find of questionable value—their place could have been taken by a simple statement of range.

The SEM photographs of spores are one of the most conspicuous features of this book, represent a primary source of new data in the classification, and deserve special comment. I was struck by the often large variation in spore ornamentation within many genera and even within species (e.g., *Cystopteris fragilis*). Such diversity leads me to question the utility of spore morphology in arriving at taxonomic judgments; at least the use of this evidence must be tempered with data from many other sources. The authors are to be commended for giving vouchers for spore photographs. However, they fail to mention sample sizes when making generalizations based on spore morphologies, e.g., the distinction between *Microlepia* and *Dennstaedtia* (p. 375).

Interspersed in the text are a few original chromosome counts (e.g., *Platycerium andinum, Trichipteris microdonta*). It is apparent that chromosome numbers also form a principal body of evidence in the Tryons' new classification. There is an inclination to refer to ancestral base numbers for some groups, despite the lack of convincing evidence for such numbers (e.g., 23 from 69 for the Cyatheaceae).

In general, the authors have taken a moderate view in recognition of families, somewhere between the narrow circumscriptions of Pichi Sermolli (1977) and Ching (1940) on the one hand and Wagner (1973) on the other. Genera are circumscribed mostly in a broad sense, a position with which I generally agree; prominent examples are *Asplenium, Dryopteris, Gleichenia, Grammitis, Tectaria, Thelypteris,* and *Trichomanes*. Exceptions are the genera of the Cyatheaceae, the subject of recent monographic work by R. Tryon and students, and of the Polypodiaceae sensu stricto. I especially like the breakdown of large genera into species clusters—groups of presumably related species—with a characterization of these clusters (examples are in *Adiantum* and *Polypodium,* in addition to some of those mentioned above). There are a few surprising generic circumscriptions. For example, *Camptosorus* and *Ceterach* are accorded generic rank even though they readily hybridize with *Asplenium;* other equally distinct genera, e.g., *Antigramma,* are sunk in *Asplenium.* A similar situation is found in Pteridaceae, where *Adiantopsis* is recognized but *Aspidotis* and *Mildella* merged in *Cheilanthes*. Therein, *Cheilanthes siliquosa* has been placed in a different species group than *C. californica,* even though they are so closely related that they hybridize to produce a fertile allopolyploid, and juveniles of all three are almost indistinguishable. In the same family, the authors postulate a relationship between *Llavea* and *Lygodium* (p. 310), citing as evidence the similarity in spores and chromosome number; the chromosome number here seems like spurious evidence and the spores of *Llavea* actually appear more similar to those of certain other cheilanthoid genera, e.g., *Cryptogramma*.

The chief fault of most recent classifications is insufficient evidence. The Tryons provide more documentation for their views than most have done. This alone will make their book a standard and indispensable reference for specialists and generalists alike.—*Alan R. Smith, Department of Botany–Herbarium, University of California, Berkeley, CA 94720.*

REVIEW

FIELD GUIDE TO MISSOURI FERNS, by J. S. Key. Missouri Dept. of Conservation, 220 pp. 1982. $3.00.—This book was written primarily for non-botanists, and so has attractive line drawings rather than keys for identification of 79 species, varieties, and forms in 28 genera found in Missouri. Introductory material includes fern morphology, collecting, preservation, and habitats. A pictorial guide using small illustrations and based mostly on frond morphology and habitat leads readers to genera. Within the genus, each taxon is illustrated with an attractive habit sketch and detailed drawings of diagnostic characters. The illustrations, plus a brief description, permit identification of the material. Each taxon has the scientific name, with an occasional synonym, the common name, and a statement of habitat and range in Missouri, as well as the description. A glossary, checklist, and an index conclude the volume. The perfect-bound book is available from the Missouri Dept. of Conservation, P.O. Box 180, Jefferson City, MO 65102. Missouri residents should add $0.12 tax.—*D. B. L.*

REVIEW

AZOLLA AS A GREEN MANURE: USE AND MANAGEMENT IN CROP PRODUCTION, by T. A. Lumpkin and D. L. Plucknett. Westview Press, Boulder, CO. xx + 230 pp. 1982. $20.00.—Although the focus of this paperback volume is agronomic, the chapter on botany and ecology (pp. 15–38) is likely to be of interest to taxonomic botanists. Illustrations and a tentative key to the species the authors recognize (*A. nilotica*, *A. pinnata* and var. *imbricata*, *A. microphylla*, *A. filiculoides*, *A. rubra*, *A. mexicana*, and *A. caroliniana*) will be useful in making identifications in this difficult genus. Most of the chapter concerns the morphology, anatomy, and life cycle of *Azolla*, and contains many illustrations. Unfortunately, the reproduction is poor, and so not much detail can be seen in the illustrations. A world-wide map showing the distribution of the *Azolla* species concludes the chapter. The bulk of the book concerns the physiology, nursery culture, field cultivation, pests, and uses in agriculture of *Azolla*. The book is available from Westview Press, 5500 Central Ave., Boulder, CO 80301.—*D.B.L.*

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Polyploidy and Aneuploidy in Hypolepis, and the Evolution of the Dennstaedtiales

P. J. BROWNSEY*

The fern genus *Hypolepis* is widespread in tropical and south temperate parts of the world. It has one center of distribution in southeastern Asia and Australasia (with a few species spreading as far as west Africa, Korea, the eastern Pacific and New Zealand) and another in the New World from the southernmost U.S.A. through Mexico and the Caribbean to Central and South America. Only one or two species of circumantarctic distribution are possibly common to both centers.

Morphologically the genus is fairly well defined, but the limits of individual species are much less obvious. Copeland (1947, p. 57) suggested that about 45 species should be recognized, although more recent investigations indicate that this is probably an underestimate. Particular problems arise in widely distributed, polymorphic taxa. These difficulties are compounded by the widespread and persistent misapplication of well known names such as *H. punctata* (Thunb.) Mett. and *H. tenuifolia* (Forst. f.) Bernh. and because many critical taxonomic features, notably the lamina and rachis hairs, are often poorly preserved or lost from old specimens, including many type collections.

The present paper is concerned with some of the wider implications resulting from a recent study of *Hypolepis* in Australia and New Zealand (Brownsey & Chinnock, in prep.). Although some of the ideas expressed here are speculative, they are put forward now in the hope of stimulating further research, particularly cytological investigation, into critical members of this group of ferns.

MORPHOLOGY

Hypolepis includes species which have the following combination of characters: rhizomes long-creeping; fronds bipinnate or more compound, often large, free-veined; hairs, glandular or bristly, on some part of the lamina, rachis, stipe or rhizome; scales absent; sorus ± round, ranging from terminal on a vein at the lamina margin, protected by a reflexed indusial flap or modified portion of the lamina, to submarginal, not quite terminating the vein, and totally unprotected; spores monolete.

These characters distinguish *Hypolepis* from allied genera, notably *Paesia*, *Pteridium*, and *Dennstaedtia*. In *Paesia*, the sori are continuous along the margins of the ultimate pinnules, borne on a marginal connecting vein, and protected both by the reflexed edge of the pinnule and by a distinct inner indusium. *Pteridium* is similar to *Paesia*, except that the inner indusium is less well developed and the spores are trilete. In *Dennstaedtia*, the spores are also trilete, but the marginal sorus is protected by a cup-shaped or slightly bivalvate indusium formed by the fusion of inner and outer indusia.

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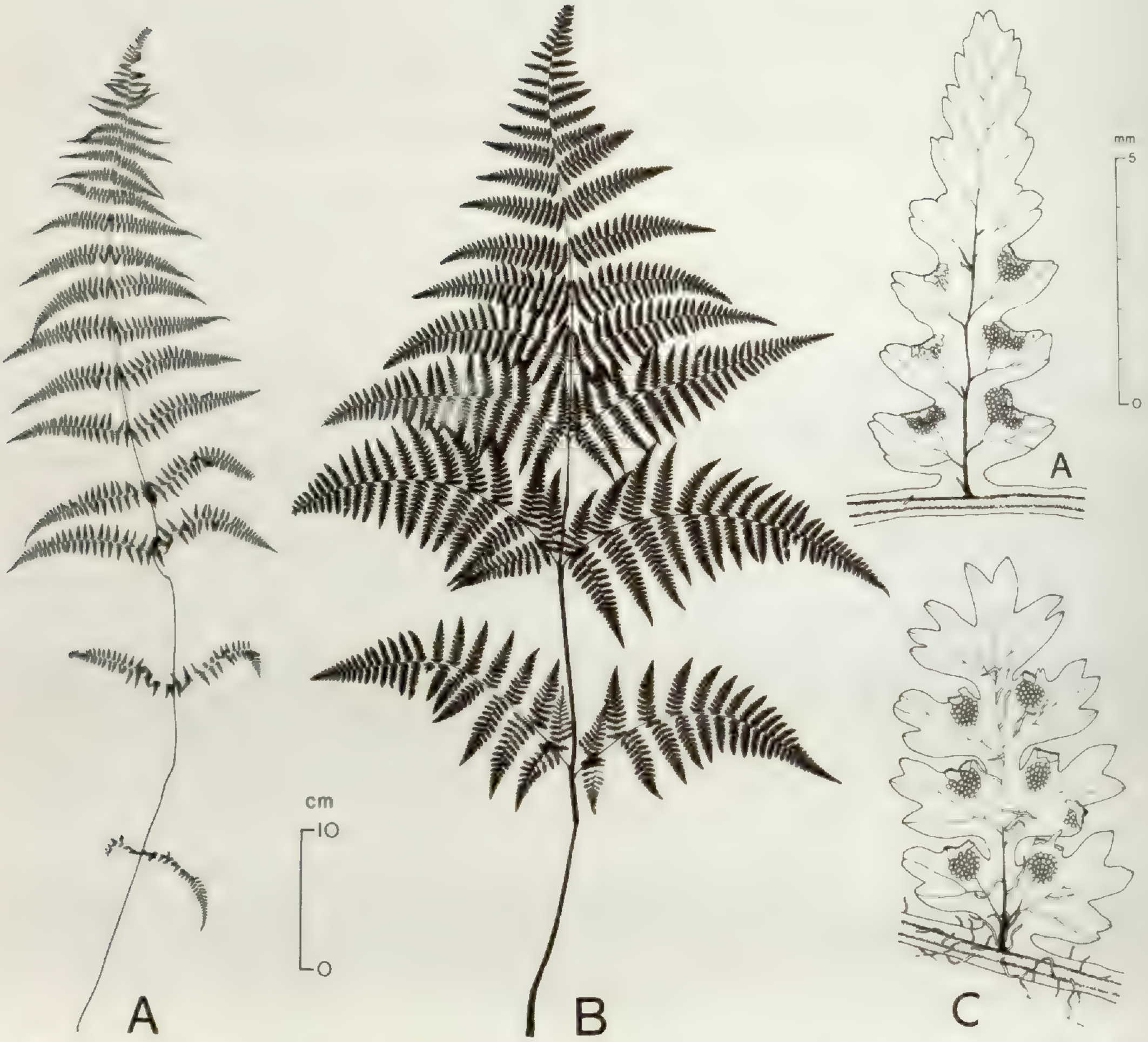

FIG. 1. Frond silhouettes and drawings of pinnules of *Hypolepis distans* (A) compared with *H. tenuifolia* sensu Allan (1961) (B) and *H. millefolium* Hook. (C).

Some species have been thought to transcend these generic boundaries. Mickel (1973) noted that an inner indusium was present in *Hypolepis bivalvis* v.A.v.R., but this taxon is better treated as *Paesia elmeri* Copel. (Holttum, 1958). More significantly, Bower (1928, fig. 587) reported the occasional presence of a vestigial inner indusium in *H. repens* (L.) Presl which he suggested linked *Hypolepis* with the Dennstaedtioid ferns, but this observation requires further investigation.

Many *Hypolepis* species are rather similar and must be distinguished by combinations of a few vegetative characters. In some cases, a well developed indusial flap is characteristic, but mostly their sori are unprotected. The hairs on the underside of the lamina are a key distinguishing character, varying in length, color, position, and glandularity. Also important are the degree of pinna dissection and the stipe and rachis color.

In Australia and New Zealand, *H. distans* Hook. stands out as being markedly different from the other ten or eleven species. The laminae are oblong-lanceolate and somewhat coriaceous, rather than characteristically deltoid and membranaceous;

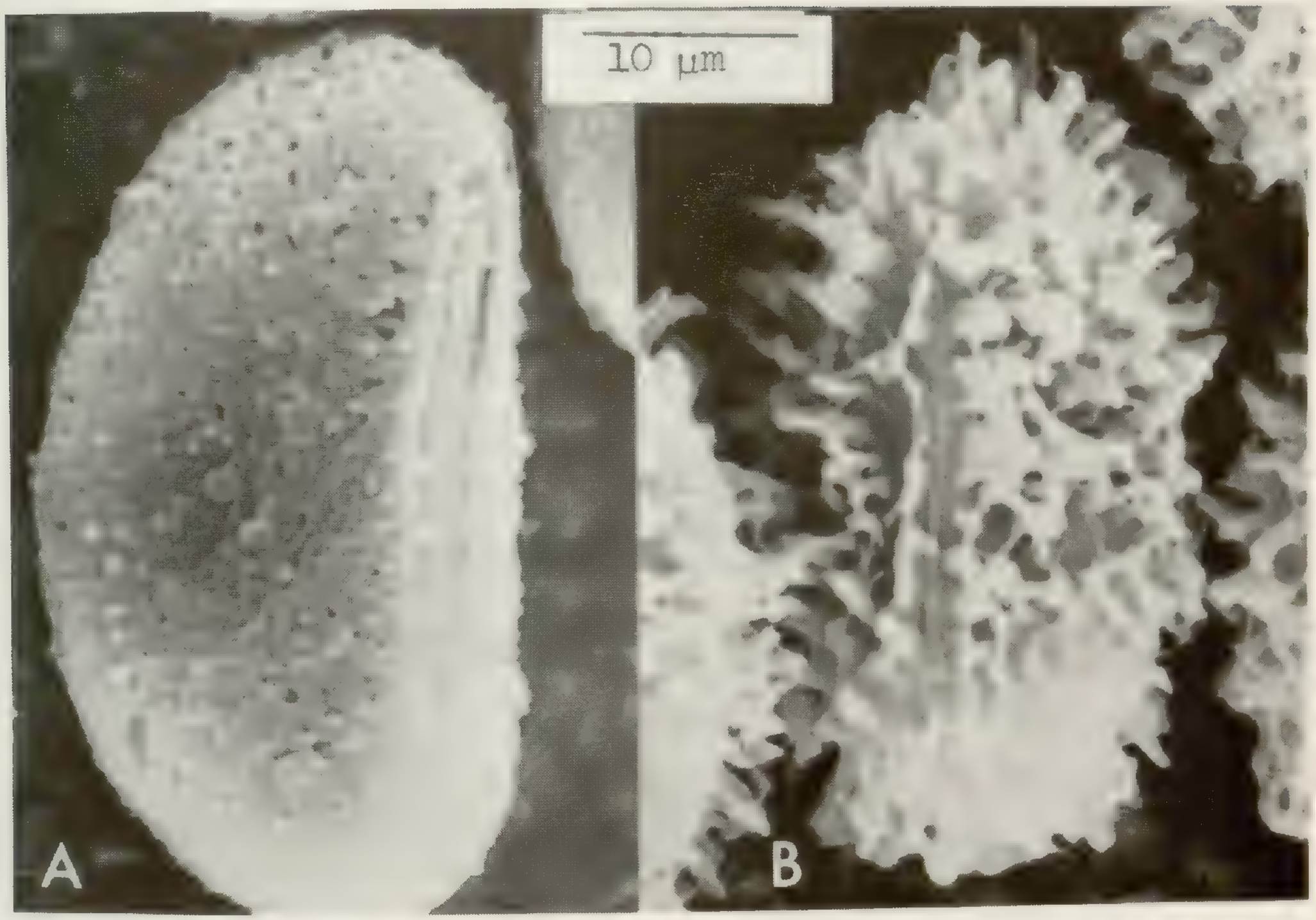

FIG. 2. Scanning electron micrographs of spores of *Hypolepis distans* (A) with a rather smooth perispore, and *H. rufobarbata* (Col.) Wakef. (B) with a perispore bearing numerous flattened projections.

the lower pinnae arise at 90° to the rachis (*Fig. 1A*), not at the usual acute angle (*Fig. 1B*); the stipes are very thin and highly polished, rather than generally thicker and hispid; and there are very few hairs anywhere on fronds of *H. distans*, which is unusual for *Hypolepis*. Most importantly, the veins of the ultimate pinnules end in emarginations (*Fig. 1A*) rather than in lobes (*Fig. 1C*). Finally, the spores of *H. distans* are very distinct, being dark brown and lacking any marked projections, in contrast to the spores of other species, which are pale and bear quite long, flattened projections (*Fig. 2*).

Species rather similar to *H. distans* are found in the New World, notably *H. nigrescens* Hook., which ranges from southern Mexico through Central America and the Caribbean to Colombia and Brazil, and the doubtfully distinct *H. hispaniolica* Maxon from the Dominican Republic and Haiti. *Hypolepis nigrescens* resembles *H. distans* in having coriaceous fronds, relatively few hairs on the lamina, pinnae arising at 90° to the rachis, veins ending in emarginations, and dark spores. On the other hand, it has rather thick stipes, which are pubescent and armed with sharp prickles, and spores which bear very fine spines. In these characters, *H. nigrescens* more closely resembles a distinctive group of *Hypolepis* species from southeast Asia represented by *H. brooksiae* v.A.v.R. and *H. papuana* Bailey. Like *H. nigrescens*, these species have a scrambling habit and periodic dormancy of the rachis (Holttum, 1958). Furthermore, their veins have a slight tendency to end in emarginations, but this is by no means so pronounced as in either *H. distans* or *H. nigrescens*. To what extent these three elements are related is not entirely clear from morphology alone.

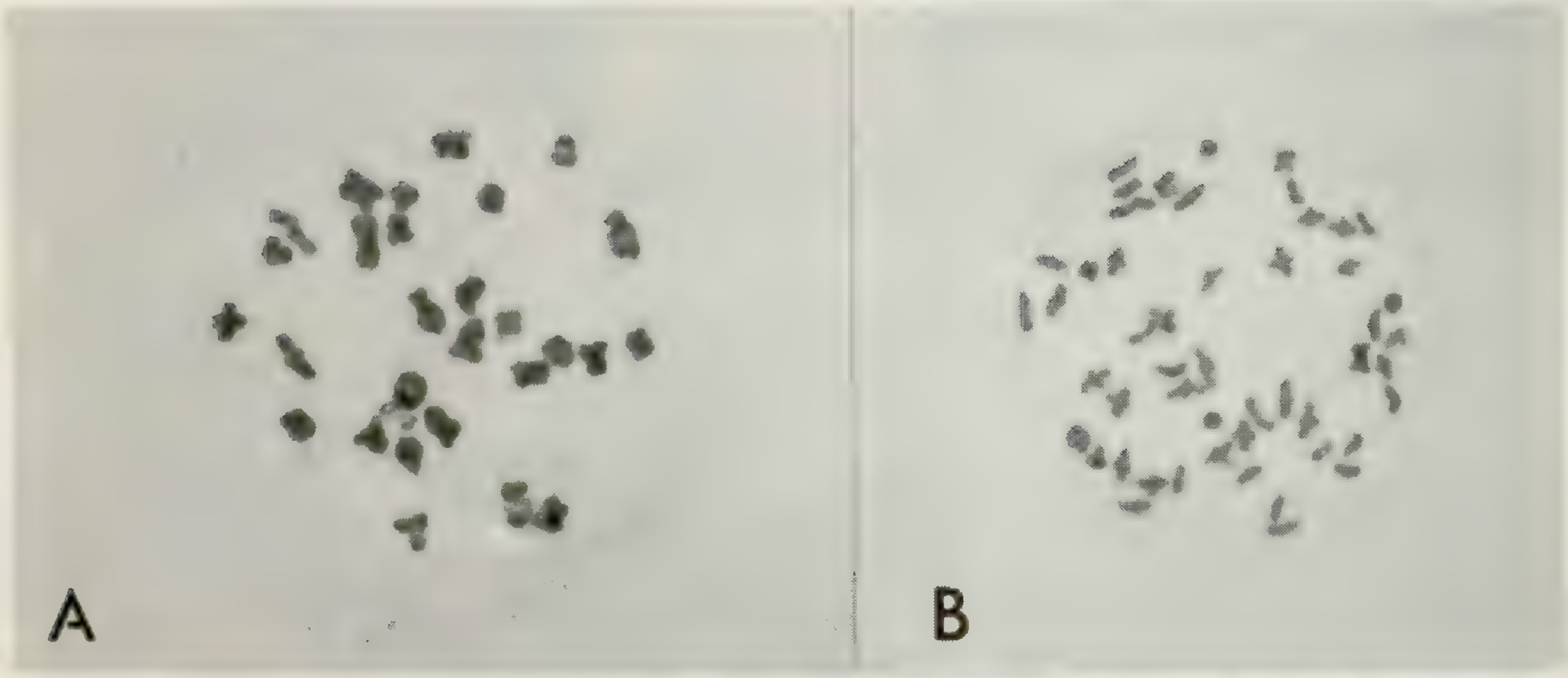

FIG. 3. Meiotic chromosome preparations (× 1000) from *Hypolepis distans* (A) Lake Kopureherehere, Levin, New Zealand, showing 28 bivalents, and *H. rufobarbata* (B) Kaituna Spur, Banks Peninsula, New Zealand, showing 52 bivalents. Voucher specimens in WELT.

HYBRIDIZATION AND CYTOLOGY

Evidence is accumulating that species of *Hypolepis*, like those of *Asplenium*, *Dryopteris* and *Polystichum*, have a considerable capacity for hybridization. There is good cytological evidence for this at different levels of ploidy among New World species of the genus and also in isolated records from Australia and Japan (*Table 1*). In New Zealand, hybridization in *Hypolepis* has long been suspected (Carse, 1929; Cockayne & Allan, 1934), and my own morphological and cytological investigations confirm this. Hybrids are recognizable by their intermediate morphology, shrivelled spores, and by the irregular pairing of their chromosomes at meiosis. Five of the six species of *Hypolepis* occurring on the main islands of New Zealand whose distributions overlap have been found to hybridize. Only *H. distans* does not appear to hybridize, which suggests, in common with the morphological and cytological evidence, that it is fundamentally distinct from the other native species.

My own unpublished results together with those of Brownlie (1954, 1957, 1958, 1961) indicate that of the six New Zealand species of *Hypolepis* other than *H. distans*, four have $n=52$ (*Fig. 3B*) and two $n=104$. By contrast, plants from four populations of *H. distans* have $n=28$ (*Fig. 3A*). Furthermore it is noteworthy that the chromosomes of *H. distans* are markedly larger than those of other New Zealand species (cf. *Figs. 3A* and *3B*).

Previously published cytological reports relating to species other than those in New Zealand are summarized in *Table 1*. All identifications are those of the original authors. Reports showing irregular meiotic pairing have been segregated as putative hybrids.

TABLE 1. CHROMOSOME COUNTS FOR SPECIES OF *HYPOLEPIS* FROM AREAS OTHER THAN NEW ZEALAND

Species	*Origin*	*n*	*2n*	*Reference*
		OLD WORLD		
H. punctata	Japan	c. 104	-	Kurita, 1962
	Japan	98	-	Kurita, 1967, 1972
	Japan, Obarano	c. 92	-	Mitui, 1968
	Japan, Saitama Pref.	98	-	Mitui, 1975
	Japan, Niigata Pref.	98	-	Mitui, 1976
	Taiwan	52	-	Tsai, 1973
	Himalayas, Darjeeling	c. 102	-	Mehra & Khanna, 1959
	Himalayas, Mussoorie	104	-	Mehra & Verma, 1960
	Nepal, Kathmandu Valley	104	-	Roy et al., 1971
	Ceylon, Hakgala	51–53	-	Manton & Sledge, 1954
	Malaya, Taiping Hills	c. 100	-	Manton & Sledge, 1954
	Malaya, Taiping Hills	c. 104	-	Manton in Holttum, 1954
	Malaya, Fraser Hills	c. 104	-	Manton in Holttum, 1954
H. tenuifolia	Samoa	-	104	Manton & Vida, 1968
H. villoso-viscidum	Gough Island	c. 100	-	Manton & Vida, 1968
H. sp.	Australia	98	-	Kurita, 1972
Hybrids				
——	Australia	-	c. 150	Manton & Sledge, 1954
"H. punctata × alte-gracillima"	Japan	meiosis irregular	c. 200	II + I Kurita, 1967, 1972
		NEW WORLD		
H. repens	U.S.A., Florida	104	-	Wagner & Chen in Löve & Solbrig, 1964
	Costa Rica, Platanillo	52	-	Smith & Mickel, 1977
	Puerto Rico, El Verde	39	-	Sorsa in Fabbri, 1965
H. viscosa	Mexico, Oaxaca	52	-	Smith & Mickel, 1977
H. nigrescens	Mexico, Oaxaca	29	-	Mickel et al., 1966
	Jamaica, Caledonia Peak	29	-	Walker, 1966
	Jamaica, Hardwar Gap	29	-	Walker, 1966
Hybrids				
"H. bogotensis"	Mexico, Chiapas	50II + 54 I	-	Smith & Mickel, 1977
"H. aff. repens"	Costa Rica, Platanillo	49II + 50 I	-	Smith & Mickel, 1977
"H. aff. viscosa"	Costa Rica, Cerro de la Muerte	52II + 52 I	-	Smith & Mickel, 1977

The majority of *Hypolepis* species so far investigated have chromosome complements of either $n=52$ or 104. The various reported numbers for collections identified as *H. punctata* and *H. repens* strongly suggest that these taxa are ill-defined. My own morphological investigations suggest that counts for "*H. punctata*" may belong to as many as four different species from Japan and northern India, Taiwan, Ceylon, and Malaya, although without access to voucher material this cannot be verified. In the New World, there is clear evidence of polyploidy in *H. repens*, and it is also likely in the *H. bogotensis/viscosa* complex (*Table 1*), although

actual counts of $n=104$ have yet to be demonstrated. Similarly, in Australia, the count from the hybrid plant with $2n=$ c. 150 strongly suggests the presence of parental species with $n=52$ and 104.

Of the anomalous numbers, the most improbable is $n=39$ for *H. repens* from Puerto Rico which must be compared with $n=104$ for the same species in Florida and $n=52$ from Costa Rica. Such divergent numbers within a single species complex are hard to accept, notwithstanding their arithmetical relationship based on 13 and the undoubted fact that *H. repens* in Central and South America is an ill-defined aggregate (Stolze, 1981, p. 280).

Another curious number, $n=98$ in Japanese plants of *H. punctata,* must be taken more seriously since it has been consistently reported from several populations and illustrated at least three times (Kurita, 1967, 1972; Mitui, 1975, 1976). Presumably it has arisen by aneupoidy, either by direct reduction from a parental species with $n=104$, or, earlier in its evolutionary history, from one with $n=52$ (i.e. 52 to 49 to 98). The cells illustrated by Kurita (1972, fig. 11) and Mitui (1976, fig. 5) show some disparity in the size of individual bivalents consistent with the idea of reduction in chromosome number by fusion. Further investigation is required to ascertain the geographical distribution of this cytotype and the extent to which the loss of chromosomes is reflected in its external morphology. From a nomenclatural point of view, it is significant that the type of *H. punctata* is from Japan.

The report of $n=29$ in *H. nigrescens* cannot be seriously doubted, having been independently reported by Mickel et al. (1966) from Mexico and by Walker (1966) from two populations in Jamaica. Furthermore, the number can now be very satisfactorily related to the discovery of $n=28$ in *H. distans* from New Zealand. However, what is not known is whether there is a direct relationship between these two species, or whether they represent fragments of quite different aneuploid lines. While the morphological and cytological evidence confirms that *H. distans* and *H. nigrescens* (and probably also the *H. brooksiae/papuana* aggregate) are significantly different from most other members of the genus, it does not yet resolve the relationship between the three elements.

In summary, these cytological observations point to a base number of $x=26$ in *Hypolepis*, despite the fact that such a number has yet to be recorded for the genus. There is a well established polyploid line of evolution represented by the numbers $n=104$ and 52 that is almost certainly derived from $n=26$, and there is the more recently demonstrated evidence of aneuploidy, with $n=29$ in *H. nigrescens* and $n=28$ in *H. distans*, that can also be related to $n=26$ (*Fig. 4*). The former existence of $n=26$ in *Hypolepis* is indirectly supported by cytological observations from *Paesia*, where the numbers $n=26$ and 104 have been reported, and from *Pteridium*, where $n=26$, 52, and 104 are all known (for original references see Löve, Löve & Pichi Sermolli, 1977, p.189). Although a base as low as 13 is theoretically possible, it seems highly unlikely unless the count of $n=39$ from Puerto Rican plants of *H. repens* can be confirmed. On the other hand there is a strong possibility that the primitive number in the genus may actually be 29, from which species having $n=26$ were derived by aneuploidy, ultimately giving rise to a successful polyploid line of evolution radiating at the tetraploid and octoploid levels.

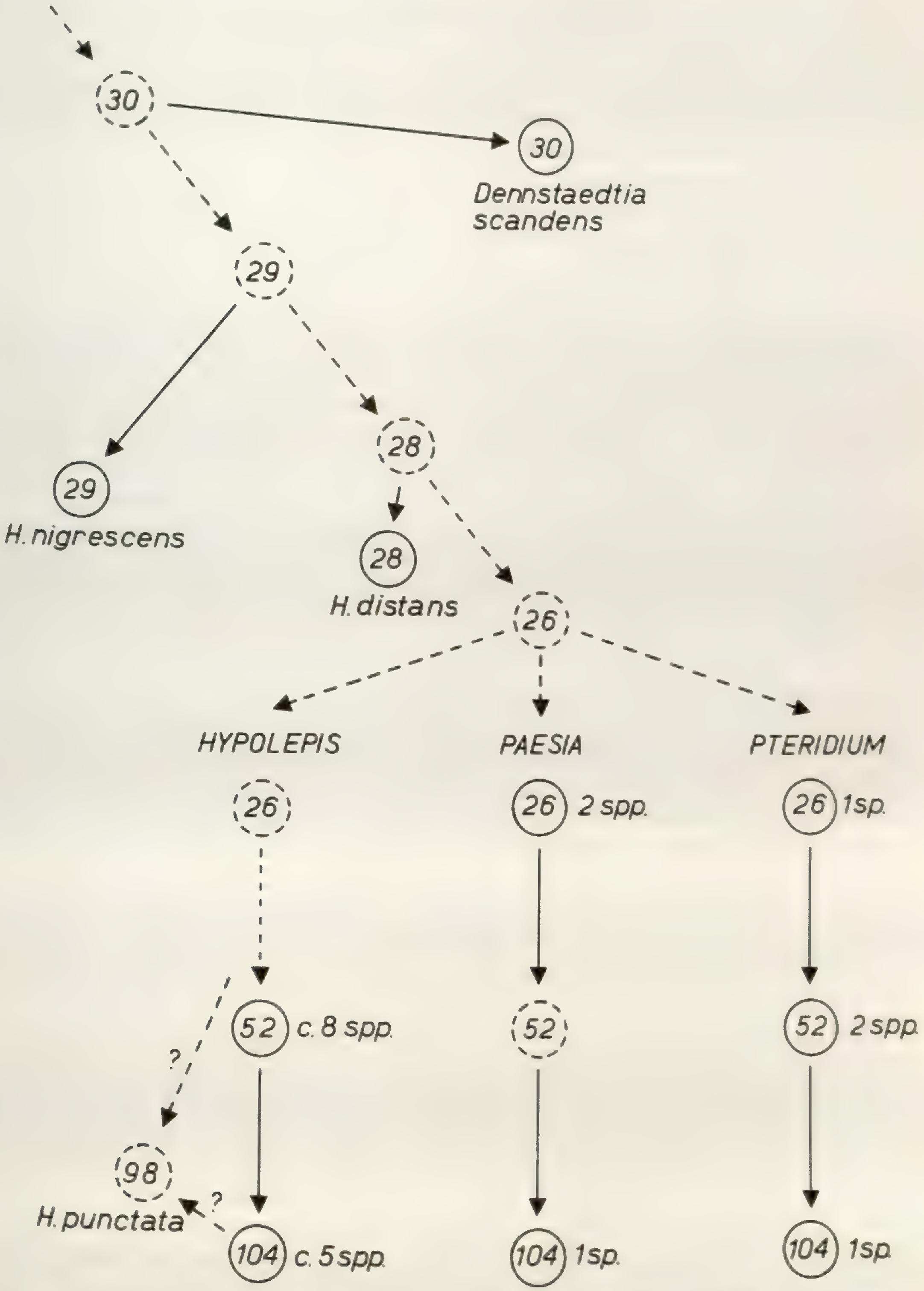

FIG. 4. Phyletic scheme deriving the Hypolepidaceae from the Dennstaedtiaceae. Solid lines and numbers in unbroken circles indicate probable lines of evolution and established chromosome numbers. Broken lines and numbers in broken circles indicate possible lines of evolution and doubtful or postulated cytotypes.

PHYLOGENETIC CONSIDERATIONS

Mickel (pers. comm.) has pointed out that the spores of *H. distans* are more similar in their perispore pattern to those of *Paesia* than to any species of *Hypolepis*, including *H. nigrescens*. He recognized some similarity in frond form between *H. distans* and the species of *Paesia* and suggested that it could be part of an aneuploid series in *Paesia* which has resulted in the loss of the characteristic inner indusium. Despite the similarity of its spores to *Paesia*, I do not believe that this alone provides sufficient evidence for regarding *H. distans* as a species of *Paesia*. In all other characters it is consistent with *Hypolepis* rather than *Paesia:* the inner indusium is absent; the sorus terminates a single vein; the veins are conspicuous (in *Paesia* they are difficult to see); the veins end in emarginations (rare in *Hypolepis*, but unknown in *Paesia*); the hairs are scarce and non-glandular (in *Paesia* they are usually abundant and glandular); and the rachis is straight, bearing pinnae which arise at right angles in more or less opposite pairs (in *Paesia* it is characteristically zig-zag bearing pinnae which arise alternately at an acute angle). Holttum (1958) related the shape of the rachis to periodic dormancy of the apex, pointing out that in *P. elmeri* the rachis rests while a single pinna develops in turn, but that in *H. brooksiae* and other genera showing periodic dormancy, a pair of pinnae develop together while the rachis rests.

Although, in my opinion, *H. distans* is closer to the polyploid species of *Hypolepis* (with $n=52$ or 104) than to species of *Paesia*, there is no doubt that all three groups are very closely related. Nevertheless, *H. distans*, with or without *H. nigrescens* and *H. brooksiae*, constitutes a distinctive element. Smith (1981, p. 136) has already noted the cytological heterogeneity of the genus and suggests that "*Hypolepis* as presently circumscribed may be unnatural." There is certainly a strong case for distinguishing the aneuploid species from the polyploid, but whether such taxonomic recognition should be at the generic or subgeneric level, and whether the aneuploid species themselves constitute a natural grouping, are very much more difficult questions to answer. For the moment, no change is proposed, and *Hypolepis* is interpreted here in a broad sense.

The question arises as to whether the aneuploid species of *Hypolepis* provide a link with other allied genera, or whether they are merely the end products of divergent evolution from an ancestral stock with $n=26$. *Paesia* and *Dennstaedtia* are central to any consideration of this possibility. Copeland (1947, p. 57), Holttum (1949), and Mickel (1973) have pointed to the similarity between *Hypolepis* and *Dennstaedtia*, Copeland in particular remarking "The more primitive element in [*Hypolepis*] . . . is hardly distinguishable from a similar element in *Dennstaedtia*." Species of the two genera share many vegetative characters, although in my experience the indusial and spore characters will always distinguish them. Nevertheless, the presence of an aneuploid line in *Hypolepis* including the numbers 28 and 29 is of considerable interest since it ties in remarkably with the numbers 30–34, 46, and 47 so far known in *Dennstaedtia* (Lovis 1977, p. 275; Löve et al. 1977, p. 184). These numbers have already been cited by Lovis (1977, p. 303) in postulating that the evolution of the Dennstaedtiaceae (i.e., Pichi Sermolli's Dennstaedtiales) is the result of a long series of aneuploid reductions from a base in the Cyatheaceae.

It may be more than mere coincidence, therefore, that *Hypolepis brooksiae* bears a quite extraordinary morphological similarity to *Dennstaedtia scandens* (Blume) Moore. In the field both are scrambling, thicket-formers with periodic dormancy of the rachis (Holttum, 1958); in the herbarium they can be distinguished only by a very careful scrutiny of the indusium or by the spores. It is highly significant that Tsai (1973) has reported the chromosome number of *D. scandens* in Taiwan to be $n=30$. Unfortunately, the chromosome number of *H. brooksiae* is not yet known, but if, as its morphological similarity to *H. distans* and *H. nigrescens* suggests, the number proves to be in the high 20's, this would constitute good evidence of an evolutionary link between *Dennstaedtia* and *Hypolepis*.

Some features of *H. distans*, notably the pronounced emarginations, the thin, highly polished stipes, and the virtually glabrous fronds, are not typical of *Dennstaedtia*. One possible answer to this paradox may be that *H. nigrescens*, *H. distans*, and perhaps *H. brooksiae*, represent remnants of unstable karyotype combinations thrown up in the course of a series of aneuploid reductions from a source in *Dennstaedtia* extending back to at least $x=34$ and possibly as far as $x=47$. An unbroken series of base numbers from 34 in *Dennstaedtia punctilobula*, through 33 or 32 in *D. scabra*, 31 in *D. wilfordii*, 30 in *D. hirsuta* and *D. scandens*, 29 in *Hypolepis nigrescens*, and 28 in *H. distans*, ultimately giving rise to a felicitous combination of 26 chromosomes in *Paesia*, *Pteridium*, and the polyploid species of *Hypolepis*, is an entirely plausible evolutionary pathway (*Fig. 4*). The very fact that many of the same characters appear in different combinations in the four genera reinforces the belief that these genera do share a common origin. For example, *Dennstaedtia*, *Paesia* and *Pteridium* have an inner indusium, but *Hypolepis* does not; *Dennstaedtia* and *Hypolepis* have sori terminating a single vein, whereas *Paesia* and *Pteridium* have sori linking several veins; *Dennstaedtia* and *Pteridium* have trilete spores, whereas *Hypolepis* and *Paesia* have monolete spores.

LIMITS OF THE HYPOLEPIDACEAE

The possibility that members of the Hypolepidaceae were derived from a source in the Dennstaedtiaceae necessitates a more careful consideration of the genera which constitute the former family. There is no doubt in my mind that *Hypolepis*, *Paesia*, and *Pteridium* form a natural group of genera with a common ancestry based on $x=26$ and that they are related to—and possibly derived from—*Dennstaedtia*, but I find it much more difficult to ally them with some of the other genera which have been referred to the Hypolepidaceae.

The family was first circumscribed and its relationships outlined by Pichi Sermolli (1970, 1977, p. 431). He included in it *Hypolepis*, *Paesia*, *Pteridium*, *Histiopteris*, *Lonchitis*, and *Blotiella*. To these (as subfamily Hypolepidoideae of the Dennstaedtiaceae) Lovis (1977, p. 276) added *Monachosorum*, *Taenitis*, and *Idiopteris*, although most workers would now probably agree that the latter two genera are better placed with the Gymnogrammeoid and Pteridoid ferns, respectively.

The true affinities of *Monachosorum* have never been satisfactorily established, but it fits no better in the Hypolepidaceae than in any of the other families to which it has been assigned (Christensen, 1938; Holttum, 1947; Copeland, 1947, p. 51;

Mickel, 1973). Lovis's main reason for putting it with the Hypolepidaceae was the belief that $n=56$ in *M. maximowiczii* (Bak.) Hayata might have been derived from $x=28$, which relates to known numbers in *Hypolepis*.

Lonchitis and *Blotiella* have also been regarded as somewhat discordant elements in the Hypolepidaceae, both by Mickel (1973) and even by Pichi Sermolli (1977, p. 432). Their chromosome numbers ($n=50$ and 38) do not fit at all comfortably.

There remains the genus *Histiopteris*, which Mickel (1973) and Pichi Sermolli (1977, p. 432) found no difficulty in allying to *Hypolepis*, *Paesia*, and *Pteridium*. However, Copeland (1947, p. 60) considered it related to *Pteris*, and Holttum (1973) included it in his list of genera whose relationships need "fresh examination." My own experience of *Histiopteris* in New Zealand suggests that it is not closely allied to other members of the Hypolepidaceae. The presence of scales on the rhizome, glaucous and virtually glabrous fronds, anastomosing veins, and sessile pinnae are all characters alien to *Hypolepis*, *Paesia*, and *Pteridium*. Most importantly, the known chromosome numbers of $n=48$ and 96 (Löve et al. 1977, p. 191) cannot easily be related to a base of 26 in the other genera.

Assuming that *Monachosorum*, *Lonchitis*, *Blotiella*, and *Histiopteris*, if not members of the Hypolepidaceae, are at least Dennstaedtialean, room must obviously be found for them elsewhere. Crabbe et al. (1975, p. 155) have already proposed for *Monachosorum* a monogeneric subfamily, Monachosoroideae, within their Dennstaedtiaceae (equivalent to Pichi Sermolli's Dennstaedtiales), and a solution of this nature may be necessary for the other genera.

EVOLUTION OF THE DENNSTAEDTIALES SENSU PICHI SERMOLLI

Looking beyond the Hypolepidaceae, Wagner (1980) has recently proposed that the neotropical genus *Loxsomopsis* might have an "affinity to either the dennstaedtioid or lindsaeoid ferns" on account of its chromosome number of $n=46$. This contrasts with $n=50$ reported for *Loxsoma* (Brownsey, 1975), a genus previously considered very close to *Loxsomopsis* but whose relation to other genera has always been very uncertain. Investigation of its gametophytes by Stokey and Atkinson (1956) and of its stomata by van Cotthem (1970, 1973) suggested an affinity between Loxsomaceae and Cyatheaceae, but the cytological evidence indicates that any such relationship must be fairly remote. However, Lovis's (1977, p. 303) suggestion that the Dennstaedtiaceae (i.e., Pichi Sermolli's Dennstaedtiales) originated by a long series of aneuploid reductions from a source in the Cyatheaceae provides a means of reconciling these differences. If *Loxsoma* and *Loxsomopsis* are admitted to be Dennstaedtialean ferns, as at least some of their morphological characters and certainly their chromosome numbers suggest, then the distant affinity with the Cyatheaceae, hinted at by the gametophyte and stomatal characters, lends some support to Lovis's hypothesis.

It may be that the troublesome *Monachosorum* also belongs on the evolutionary line from the Cyatheaceae to the Dennstaedtiales. Its position here could help to reconcile the views of Copeland (1947), Crabbe et al. (1975), and Pichi Sermolli (1977, p. 430), who allied it with the Dennstaedtiaceae, with those of Christensen (1938), who allied it with the Thelypteridaceae; in both Holttum's (1973) and

Lovis's (1977, fig. 3) scheme, the latter family is itself an offshoot of the Cyatheaceae. Certainly the chromosome number of *Monachosorum* ($n=56$) fits better here than in the Hypolepidaceae. Moreover, the numbers 46, 50, and 56 now established in *Loxsomopsis*, *Loxsoma*, and *Monachosorum* go some way to bridging the gap between the highest confirmed number of $n=48$ in the Dennstaedtiales (Lovis, 1977, p. 304) and the range of 56–69 (excepting 95 or 96 in *Metaxya*) in the Cyatheaceae sensu Lovis (1977, p. 273).

This leaves an awkward group of genera, *Blotiella* ($n=38$), *Histiopteris* ($n=48$), and *Lonchitis* ($n=50$), whose affinities are far from clear. *Blotiella* and *Histiopteris* have much in common morphologically, but cytologically the latter genus is closer to *Lonchitis*. Tryon (1962) suggests that *Blotiella* is related to *Hypolepis*, but that *Lonchitis* is closer to *Pteris*. *Histiopteris* has also been allied with both the Dennstaedtialean and Pteridoid ferns, but its cytology fits comfortably into neither group; the Pteridoid ferns are clearly based on $x=29$ or 30, albeit with an aberration of $n=27$ in *Idiopteris*, while the known range in Dennstaedtialean ferns (26–c. 50) would require *Histiopteris* to be placed at the higher end of the cytological spectrum where its morphology is even more out of place than at the lower end with the Hypolepidaceae. The affinities of these three genera need to be more thoroughly investigated; meanwhile, I regard their placement as uncertain.

I am extremely grateful to Dr. J. E. Braggins, University of Auckland, New Zealand, for supplying me with the photograph illustrated in Figure 2, to Dr. J. T. Mickel, New York Botanical Garden, for his unpublished observations on New World species of *Hypolepis* and *Paesia*, and to Dr. Mickel and Professor J. D. Lovis, University of Canterbury, New Zealand, for their critical and extensive comments on the manuscript.

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Pecluma, a New Tropical American Fern Genus

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The species of *Pecluma* were submerged in *Polypodium* until modern taxonomists separated Grammitids from Polypods. Then, Copeland (1956) included some members of *Pecluma* in a generic treatment of the Grammitid *Ctenopteris*. That provided the impetus for three papers which supplied evidence that *Pecluma* species indeed belonged with *Polypodium* (Stokey, 1959; Wilson, 1959; Sota, 1963). A later revision of the individual species by Evans (1969) has facilitated a new examination of the relationships of the group, and I have come to the conclusion that those authors who reaffirmed an alliance with *Polypodium* are correct, but that Copeland's error may be partly excused on the grounds that *Pecluma* also has many features reflecting a shared ancestry with *Ctenopteris*, features that mark it as abundantly distinct from *Polypodium*. The most conspicuous of these differences from *Polypodium* are: rhizomes short and non-branching, paleae basally attached, axes terete, and fronds pectinate. From *Ctenopteris*, diagnostic differences are: spores neither trilete nor green, hairs never acicular from a broad base and not dark maroon, and stipes articulate. These and other characters are detailed below.

Pecluma Price, gen. nov.

Polypodium subg. *Pectinatum* Lellinger, Amer. Fern J. 71:93. 1981.

"*Polypodium pectinatum-plumula* complex" Evans, Ann. Missouri Bot. Gard. 55:193–293. 1969.

Rhizoma breve, non ramificans nec glaucescens, radices saepe prolificas procreans. Paleae basifixae, non clathratae, nec in lamina conspersae, cellulis ad margines non valde differentiatis. Stipites articulatae, rachidesque teretes, in vivis siccisve non sulcatae, atrantes. Segmenta laminae conferta, numerosa, longa angustaque, plerumque sursumdecurrentia, marginibus non cartilagineis pilis ascendentibus multiseptatis dispositis, infra pagina pilis multiseptatis glandulosis appressis praedita. Venae liberae vel fortuito anastomosantes. Stomata polocytica atque anomocytica vel copolocytica. Sori orbiculati paraphyses trichoideas continentes. Sporae monolaetae, non chlorophyllosae.

TYPE: *Polypodium pectinatum* L.

ETYMOLOGY: *Pecluma* is a compound of the epithets *pectinatum* and *plumula* which have been used to exemplify the group.

DISTRIBUTION: Tropics and subtropics of the New World, from Bermuda, Florida, and northern Mexico to southern Brazil and northern Argentina (Evans, 1969). Species about 28, generally epiphytic or epipetric.

The only previous author to accord formal taxonomic rank to *Pecluma* was Lellinger (1981), who noted that it was "sharply distinct" from the rest of *Polypodium*. As a genus, *Pecluma* is immediately recognizable and clearly defined and circumscribed. Separation from *Polypodium* (sensu stricto or lato) is important for the portrayal of the evolutionary lines involved, since *Pecluma* appears to have preserved characters that are possibly primitively simple among Polypods. Some of these character elements, especially of rhizomes, paleae, and axes, are fundamentally different from the usual condition in not only the genus *Polypodium* but also

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the entire subfamily Polypodioideae (the Polypods). The removal of *Pecluma* thus leaves *Polypodium* far more uniform, definable, recognizable, and phylogenetically meaningful. However, *Pecluma* does agree with *Polypodium* in a number of crucial features that require microscopy for detection (characters of the spores, sporangial stalks, and gametophytes), as well as the articulate stipes, which taken together are my basis for maintaining it in the Polypodioideae. In the other direction, *Pecluma* agrees with many members of subfamily Grammitidoideae in various characters by which it differs from the other genera of subfamily Polypodioideae, again characters of rhizomes, paleae, and axes, and also of frond-form and venation.

Loxogramme exhibits a mosaic of characters otherwise associated with either the Polypodioideae or the Grammitidoideae, and therefore is living evidence that those two are linked evolutionarily. A subfamily Loxogrammoideae may therefore be appropriate. I believe that *Pecluma* must be retained in subfamily Polypodioideae, rather than be placed in a subfamily of its own, but I am convinced that its numerous character states so similar to those widespread in the Grammitidoideae cannot be attributed to evolutionary convergence or reversal, but rather indicate shared ancestry. *Pecluma*, then, provides further evidence of the affinity between the Polypod and the Grammitid ferns and strengthens the case for ranking them as subfamilies of a greater Polypodiaceae, as apparently first done by Wagner (1961).

In the following discussion of the characteristics of *Pecluma*, I will not attempt to repeat the morphological observations made in the excellent paper of Evans (1969), except to place emphasis on certain character states. A summary of major characters compared with *Polypodium* and *Ctenopteris*,[1] both confused with *Pecluma* in the past, is presented in *Table 1*.

In *Polypodium*, the rhizome is wide-creeping, even rampant, regularly branching or producing short, dormant side branches, and is often glaucous beneath the paleae. *Pecluma* differs strongly in all these features, with the rhizome invariably short, whether ascending or creeping, and even when creeping having phyllopodia close together (exceptionally to 1 cm apart), and never regularly branching. The absence of rhizome branches is sometimes compensated for by the production of proliferations from the roots, already confirmed for seven species by Evans (1969, pp. 195, 196, and 203), and one more first noted here, *P. funicula*. The rhizome surface is never glaucous. All these rhizome characters, as they contrast with *Polypodium*, are the general condition of Grammitid ferns, which usually have short, non-branching, non-glaucous rhizomes, although the Malesian *Ctenopteris taxodioides* and the American *C. moniliformis*, for example, have slender, long-creeping rhizomes. Root proliferations are known among Polypods only in the highly-specialized *Platycerium*, where they should not be construed as evidence of affinity to *Pecluma*. Among Grammitids, root prolifery has only been confirmed for *Adenophorus* subg. *Oligadenus* (Bishop, 1974), perhaps first shown in the careful illustration of *A. pinnatifidus* Gaud. by Brackenridge (1855, pl. 2, fig. 3.). In the Poly-

[1]The name *Ctenopteris* is used here for expedience to refer to miscellaneous pinnate or subpinnate species of Grammitids, although its Malesian type is very closely related to the type of the earlier described genus *Prosaptia*.

TABLE 1. COMPARISON OF MAJOR CHARACTERS OF *Pecluma* WITH *Polypodium* SENSU STRICTO AND THE PINNATE OR SUBPINNATE GRAMMITIDS ("*Ctenopteris*").

Structure	*Polypodium*	*Pecluma*	*Ctenopteris*
Rhizome	long-creeping	short	usually short
	freely branching	unbranched	unbranched
	often glaucescent	not glaucous	not glaucous
Roots	not proliferous	often proliferous	sometimes proliferous
Paleae	peltately attached	basally attached	basally attached
	often clathrate	not clathrate	usually not clathrate
	sometimes with rhizoids	sometimes with rhizoids	sometimes with rhizoids
	often marginate	margin not differentiated	margin usually not differentiated
	often scattered on lamina	only along axes or absent from lamina	not on lamina
Stipes	articulate	articulate	usually not articulate
Axes	variously channeled	perfectly terete	usually terete
	usually not dark	dark	often dark
Lamina segments	usually relatively few	numerous	usually numerous
	often lanceolate	linear	usually linear
	occasionally sursumcurrent	usually sursumcurrent	occasionally sursumcurrent
Hairs	various or glabrescent	multiseptate, dense on rachis above, appressed on lamina below and glandular	various, often acicular, broad-based, dark maroon
Venation	free to regularly anastomosing	free or casually anastomosing	free or casually anastomosing
Stomates	usually polocytic + copolocytic and/or anomocytic	polocytic + anomocytic or copolocytic	usually polocytic + anomocytic
Paraphyses	scales, hairs, or apparently none	hair-like	hair-like or apparently none
Sporangial stalks	2 or 3 cells thick throughout	2 or 3 cells thick throughout	uniseriate at base
Spores	monolete	monolete	trilete
	not green	not green	chlorophyllose
Chromosome numbers	$x = 37$	$x = 37$	$x = 37$

podiaceae as here circumscribed, root prolifery is also exhibited by *Anarthropteris*, a close ally of *Loxogramme*.

Basally attached paleae characterize the Grammitids. In *Polypodium*, the ubiquitous condition is peltate attachment; even among the entire Polypodioideae, basally attached paleae occur only in a few highly specialized cases unrelated to *Pecluma*, i.e., *Platycerium*, a few large *Pyrrosia* species, and some drynarioid ferns. *Pecluma* has paleae basally attached both on the rhizomes and the fronds, and if borne on the frond they are situated only along axes, never scattered on the laminar surface, not clathrate in whole or in part, and not strongly differentiated at the margins. Some species of *Pecluma* as well as *Polypodium* and *Ctenopteris* have rhizoids on the surfaces of the rhizome scales which appear to be homologous with root hairs, and so presumably function for absorption. Marginal hairs on the paleae, when they occur in any of these three, are morphologically quite different. Surficial hairs on

the paleae are also found in *Tricholepidium* (Ching, 1978) of Pleopeltid affinity, where they resemble the slender, maroon setae of the Grammitids, in *Leucostegia* of the Davalliaceae, in *Pleurosoriopsis*, where they seem to be rhizoidal, and in the Thelypteridaceae (Holttum, 1971), where they are related to the hairs on the fronds.

Pecluma agrees with the Polypodioideae rather than the Grammitidoideae in the important character of stipes articulate to the phyllopodia, but this is not an exclusive feature, as *Ctenopteris celebica*, for example, has articulate stipes. The stipe and rachis of *Pecluma* are dark and virtually perfectly terete; they do not shrink during drying to become grooved, channeled, or differentially dimensional. No *Polypodium* has this character, although it is widespread in the Grammitidoideae, and occurs in some species of *Pleopeltis* of the Polypodioideae. In checking for this character, one must be wary of several deceptive conditions. If immature, still-developing fronds are dried before the deposition and hardening of the sclerenchymatous sheath responsible for the character, the axes will shrink along certain lines and appear to be channeled, or if unusually heavy or unequal mechanical pressure is used in drying, portions of the axes may appear slightly compressed. Laminar tissue is long-decurrent down the stipe, forming a very narrow strip on each side, but the actual shaft of the stipe is invariably terete.

Laminar segments (pinnae) are very numerous (over 40) and long and narrow, the ratio of length to breadth ranging from 6:1 to 14:1, giving the fronds a marked pectinate appearance, and although nearly the same character state occurs in a few species of *Polypodium*, the situation is far more frequent in *Ctenopteris*. In most species, some or all of the segments are sursumcurrent, the bases extending upwards along the rachis more markedly than downwards. This character is more common in *Polypodium* than in *Ctenopteris*, but occurs in both. The margins are never cartilaginously reinforced as in many Polypods.

Fronds are always hairy with multiseptate hairs, copious on the rachis adaxially, less so abaxially, and at intervals along the margins (except in *Pecluma curvans* and *P. pectinatiformis*); the lamina beneath almost always has appressed, pale, multiseptate hairs with glandular terminal cells (except *P. hygrometrica*, which has erect, non-glandular hairs). The morphology and distribution of these hairs are most similar to those of some species of *Polypodium*, and although a few *Ctenopteris* have hairs of similar appearance and distribution, the widespread condition in the Grammitidoideae of dark maroon, broad-based, slender, acicular hairs is never found in *Pecluma*.

The combinations of stomatal types are similar to those widespread among the Grammitids (van Cotthem, 1970) and Polypods (Sen & Hennipman, 1981). *Pecluma plumula* has a combination of polocytic and copolocytic stomates, whereas the other species I have examined (*P. pectinata*, *P. hygrometrica*, *P. ptilodon*, and *P. pectinatiformis*) combine polocytic with anomocytic stomates.

Sori are orbicular, never elongate as in some *Polypodium* and *Ctenopteris*, surficial (slightly impressed in *P. sursumcurrens*), and always contain hair-like paraphyses. Setose sporangia are common in *Pecluma* and *Ctenopteris*, but are rare in *Polypodium*. Wilson (1959) pointed out that although no fundamental differences exist between the sporangial capsules of Polypods and Grammitids, *P. pectinata* and

P. plumula both agree with the Polypodioideae in having two rows of cells at the base of the sporangial stalk (vs. a single row at the base in the Grammitidoideae). Spores are normally monolete and fabiform (globose in *P. dispersa*), finely tuberculate, and achlorophyllous. Spore characters are probably most consistently useful for distinguishing between subfamilies Polypodioideae and Grammitidoideae, as exceptions are very rare, and in only one case is a Grammitid known to have monolete spores (F. S. Wagner, in prep.).

Gametophyte characters agree best with *Polypodium* as to early appearance of the first rhizoid, short duration of the filamentous stage, form of the mature thallus, and distribution and types of hairs (Stokey, 1959), although gametophytes of the apogamous *Pecluma dispersa* agree with the Grammitidoideae in several characters (Evans 1969, p. 207).

Most similar to *Pecluma* is the group of species[2] around *Polypodium hartwegianum* Hook., as pointed out by Evans (1969, p. 217) and Smith (1981, p. 187), but all these species have the usual differences in rhizomes, paleae, and axes. The Old World *Thylacopteris*, a segregate of *Polypodium*, is similarly pectinate, but has a very slender, long-creeping, branched rhizome, peltate paleae, grooved axes, and glabrescent laminae.

I am indebted to Prof. W. H. Wagner, Jr. and David M. Johnson for critical comments and helpful discussion.

ENUMERATION OF SPECIES

Pecluma absidata (Evans) Price, comb. nov.
Polypodium absidatum Evans, Ann. Missouri Bot. Gard. 55:238, f. 20. 1969.

Pecluma alfredii (Rosenst.) Price, comb. nov.
Polypodium alfredii Rosenst. Fedde Repert. 22:15. 1925.

Pecluma atra (Evans) Price, comb. nov.
Polypodium atrum Evans, Ann. Missouri Bot. Gard. 55:237, f. 18. 1969.

Pecluma bermudiana (Evans) Price, comb. nov.
Polypodium bermudianum Evans, Ann. Missouri Bot. Gard. 55:228, f. 17. 1969.

Pecluma boliviana (Rosenst.) Price, comb. nov.
Polypodium bolivianum Rosenst. Fedde Repert. 5:236. 1908.

Pecluma camptophyllaria (Fée) Price, comb. nov.
Polypodium camptophyllarium Fée, Huit. Mém. 86. 1857.

Pecluma chiapensis (Evans & Smith in Smith) Price, comb. nov.
Polypodium chiapense Evans & Smith in Smith, Amer. Fern J. 70:23, f. 16–17. 1980.

Pecluma choquetangensis (Rosenst.) Price, comb. nov.
Polypodium choquetangense Rosenst. Meded. Rijks Herb. 19:18. 1913.

Pecluma consimilis (Mett.) Price, comb. nov.
Polypodium consimile Mett. Ann. Sci. Nat. (Paris) V. 2:253. 1864.

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[2]These species have often been included in *Polypodium* subg. *Goniophlebium*, but the name *Goniophlebium* when used as a subdivision of *Polypodium* is typified by an Old World species whose relationship with American species remains to be clarified.

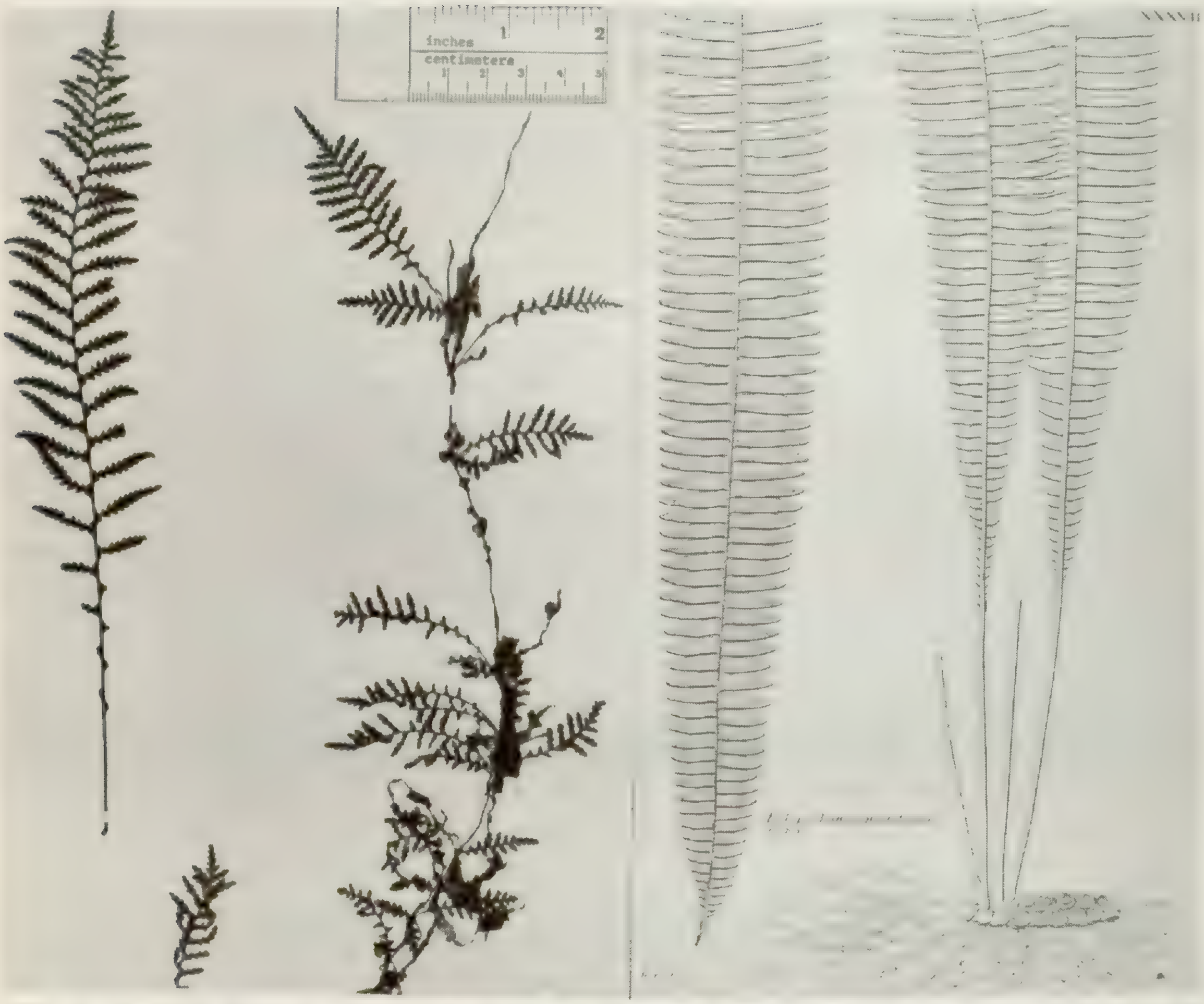

FIG. 1. *Pecluma funicula* showing a fertile frond (left) and an elongate root with a series of plantlets produced by prolifery (Oriente, Cuba, "creeping on trees," *von Eggers 5104*, MICH).
FIG. 2. Plate 37 of Plumier's "Description des Plantes de l'Amerique."

Pecluma cupreolepis (Evans) Price, comb. nov.

Polypodium cupreolepis Evans, Ann. Missouri Bot. Gard. 55:224, f. 17. 1969.

This species was reduced to *P. alfredii* by Stolze (1981, p. 395).

Pecluma curvans (Mett.) Price, comb. nov.

Polypodium curvans Mett. Ann. Sci. Nat. (Paris) V, 2:253. 1864.

Pecluma dispersa (Evans) Price, comb. nov.

Polypodium dispersum Evans, Amer. Fern J. 58:173, pl. 27. 1968.

Pecluma eurybasis (C. Chr.) Price, comb. nov.

Polypodium eurybasis C. Chr. Svensk. Vet. Akad. Handl. III, 16:71, t. 16, f. 12–13, 1937.

Pecluma ferruginea (Mart. & Gal.) Price, comb. nov.

Polypodium ferrugineum Mart. & Gal. Mém. Acad. Bruxelles 15:36, t. 6, f. 2. 1842.

Pecluma filicula (Kaulf.) Price, comb. nov.

Polypodium filiculum Kaulf. Enum. Fil. 275. 1824, as "filicula."

Pecluma funicula (Fée) Price, comb. nov.

Polypodium funiculum Fée, Gen. Fil. 241. 1852; Six. Mém. 12, t. 8, f. 2. 1854.
Ctenopteris funicula (Fée) J. Smith, Hist. Fil. 185. 1875.

This Cuban species, overlooked by Evans (1969), is one of two members of the genus *Pecluma* with deeply pinnatifid segments, the other being *P. choquetangensis*, known from only Bolivia. *Pecluma funicula* differs conspicuously by the rachis ± straight (not sinuous) and the pinnae and lobes only slightly ascending (vs. ascending at c. 45°). But the most interesting character of *P. funicula* is the rampant root system (see *Fig. 1*), freely proliferating and imitating rope-like, long-creeping rhizomes. Fée described these roots as rhizomes, and illustrated an elongate, interwined clump of roots and fronds.

Pecluma hygrometrica (Splitg.) Price, comb. nov.
Polypodium hygrometricum Splitg. Tijdschr. Nat. Gesch. 7:409. 1840.

Pecluma paradiseae (Langsd. & Fisch.) Price, comb. nov.
Polypodium paradiseae Langsd. & Fisch. Icon. Fil. 11, t. 11. 1810.

Pecluma pectinatiformis (Lindm.) Price, comb. nov.
Polypodium pectinatiforme Lindm. Hedwigia 43:309. 1904.

Pecluma pectinata (L.) Price, comb. nov.
Polypodium pectinatum L. Sp. Pl. 1085. 1753.

This species provides the type of the genus. Its lectotype, chosen by Evans (1969, p. 246), is plate 37 of Plumier's (1693) "Description des Plantes de l'Amerique" (*Fig. 2*).

Pecluma plumula (Humb. & Bonpl. ex Willd.) Price, comb. nov.
Polypodium plumula Humb. & Bonpl. ex Willd. Sp. Pl. ed. 4, 5:178. 1810.

Pecluma ptilodon (Kunze) Price, comb. nov.
Polypodium ptilodon Kunze, Linnaea 9:42. 1834.

Evans (1969) divided this species into four varieties, two of which are tetraploids. If the two tetraploids are united into a distinct entity, as they were by Löve & Löve (1977), the earliest name for it is *Polypodium robustum* Fée.

Pecluma recurvata (Kaulf.) Price, comb. nov.
Polypodium recurvatum Kaulf. Enum. Fil. 106. 1824.

Pecluma sicca (Lindm.) Price, comb. nov.
Polypodium siccum Lindm. Ark. Bot. 1:234, t. 11, f. 4. 1903.

Pecluma singeri (de la Sota) Price, comb. nov.
Polypodium singeri de la Sota, Opera Lilloana 5:181. 1960.

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The Lady Fern, Athyrium filix-femina, in Saskatchewan

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Several years ago, Harms (1978) reported the first Saskatchewan records of the Lady Fern, *Athyrium filix-femina* (L.) Roth, from the Wollaston Lake–Reindeer Lake region in the northeastern part of the province. These collections partially filled in an apparent mid-continental distribution gap of over 1300 km from central Manitoba to westernmost Alberta, between the known eastern and western ranges of *A. filix-femina* s.lat. in northern North America (*Figs. 1*, D and *2*).

During the last several years, 13 additional collections (with duplicates, including 84 individual plants) of *A. filix-femina* have been made from five widely separated regions of Saskatchewan, plus one collection from northeastern Alberta. These greatly expand the known range of the species in the province and in west-central Canada (*Figs. 1* and *2*). The six general regions (and in parentheses the more specific localities within each) for collections of the Lady Fern in Saskatchewan now include the following: (1) Wollaston Lake–Reindeer Lake (Hidden Bay of Wollaston Lake, Geikie River, Courtenay Lake, and W of Numabin Bay of Reindeer Lake; previously reported in Harms, 1978); (2) Cypress Hills (Boiler Creek north of Loch Leven); (3) Clearwater River (Smoothrock Falls and Descharme River); (4) Lake Athabasca south shore (Cantara Bay and MacFarlane River); (5) Wapawekka Hills (north slope above and below abandoned military site); and (6) the Pasquia Hills (S. Fork White Poplar Creek and N. Fork Stony Creek). The above regions are indicated by letter-symbols on the Saskatchewan distribution map (*Fig. 1*), and the actual collection sites by dots (to the extent the sites are far enough apart to be distinguishable as separate dots at the scale of the base map). The new collections are those of the author with Robert A. Wright et al., except for the Cypress Hills collection, which was made by W. C. Harris and S. M. Lamont. The single collection from northeastern Alberta was from along the Clearwater River 24 km west of the Saskatchewan border (15 June 1979, *Wright s. n.*), and essentially fits into our general Clearwater River region (*Fig. 1*, B). Vouchers of all collections are deposited in The W. P. Fraser Herbarium (SASK). Complete collecting data for these is available upon request from the Herbarium or the author.

The local abundance of *A. filix-femina* at most Saskatchewan sites was surprising, considering that the species had not previously been reported from the province. Our floristic studies in the Pasquia Hills and Wapawekka Hills revealed this to be one of the more frequent ferns at higher elevations, third in abundance only to *Matteuccia struthiopteris* (L.) Todaro and *Dryopteris spinulosa* (O. F. Muell.) Watt. Lady Ferns appear to have been overlooked previously in Saskatchewan, possibly mistaken in the field for the Spinulose Shield Fern, *D. spinulosa*, to which at least the western forms bear a cursory resemblance. But even vegetatively, Lady Ferns may be distinguished from the latter by their veinlets extending to tips of the pinnule teeth and their teeth tips not being truly spinulose. In the Pasquia and Wapawekka Hills, *D. spinulosa* tended to be rather more characteristic of upland coniferous woods, in contrast to

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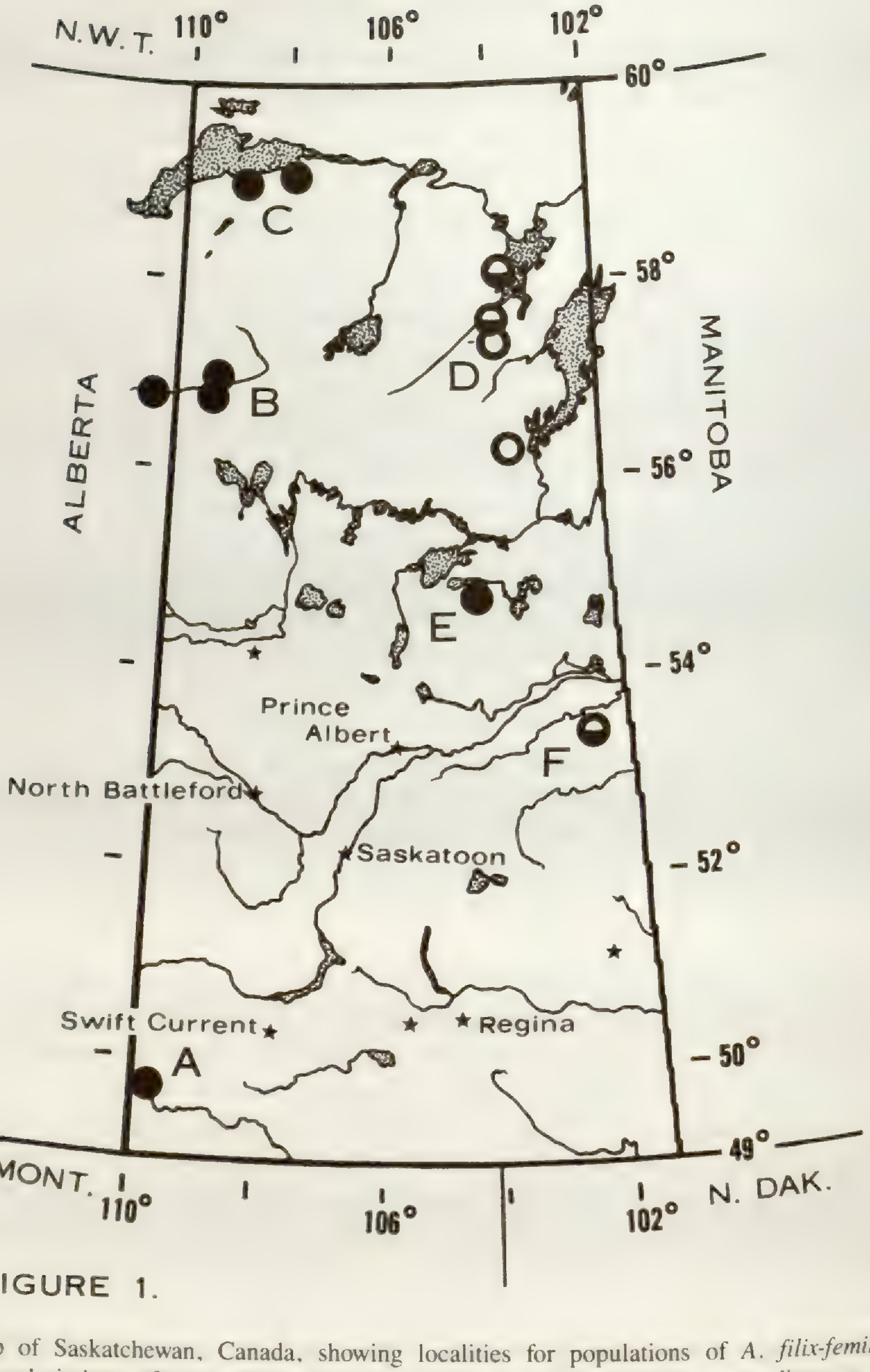

FIGURE 1.

FIG. 1. Map of Saskatchewan, Canada, showing localities for populations of *A. filix-femina* var. *sitchense* (closed circles), of var. *michauxii* (open circles), and of those with intermediates as well as var. *sitchense* (half-open circles). Symbols for the regions are: A = Cypress Hills Provincial Park, B = Clearwater River, C = South shore of Lake Athabasca, D = Reindeer Lake–Wollaston Lake, E = Wapawekka Hills, and F = Pasquia Hills.

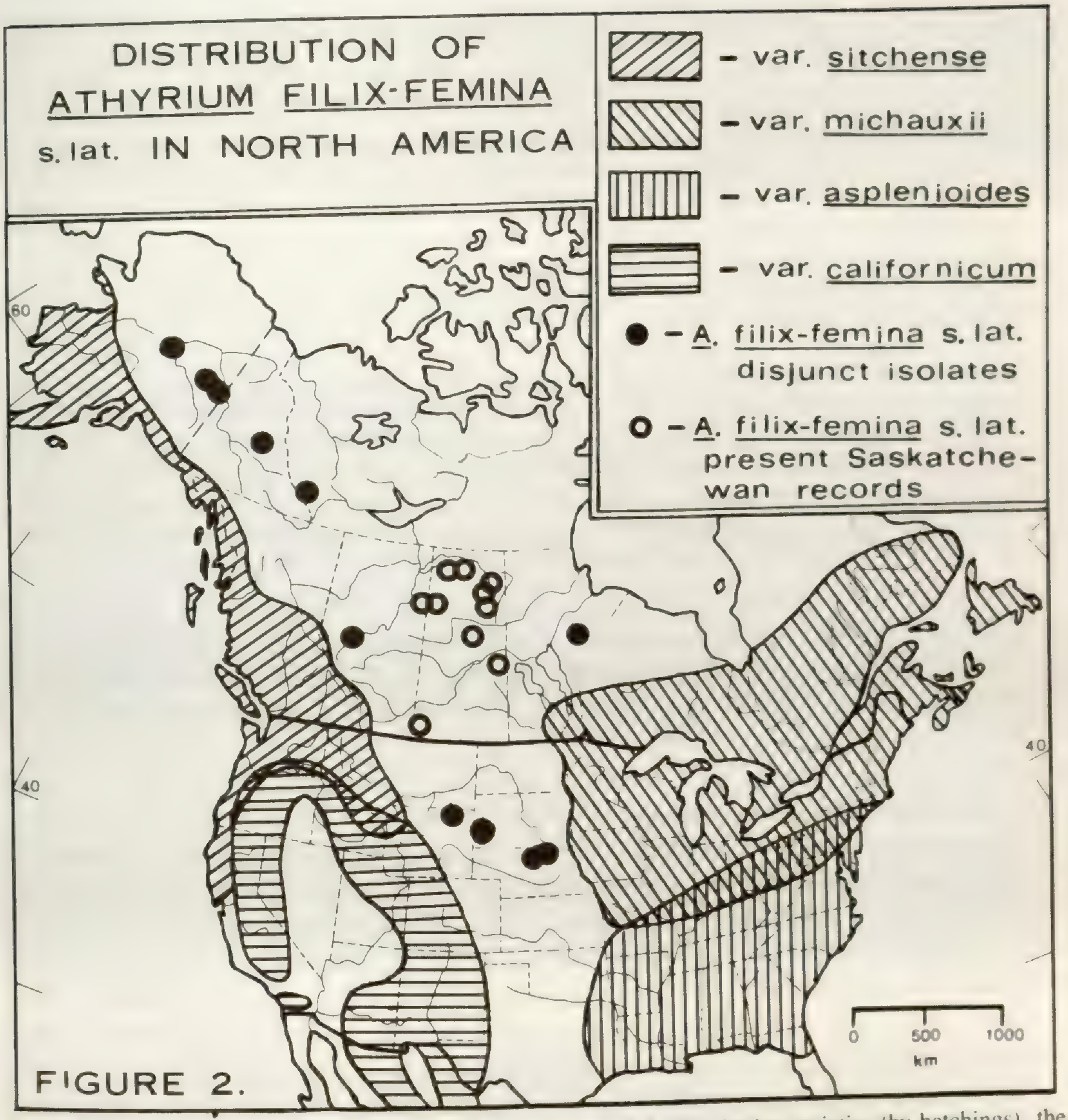

FIG. 2. Map of North America showing the main ranges of *A. filix-femina* varieties (by hatchings), the location of previously reported disjunct isolates (by closed circles), and the presently reported Saskatchewan collections (by open circles), indicating the geographical relationship of the new records to the former. Based mainly on Hultén (1964, pp. 178–179, 1968, p. 48), but supplemented by information from McGregor et al. (1977, p. 5), Scoggan (1957, p. 63, 1978, pp. 155–156), Boivin (1967, pp. 29–30), Gleason and Cronquist (1963, p. 17), and Hitchcock et al. (1969, pp. 63–64).

the usual Lady Fern habitat here and elsewhere in the province of moist, mixed-wooded or shrub-thicketed to more or less open stream sides, lake shores, and seepage areas.

The Saskatchewan specimens of *A. filix-femina* are especially interesting because they occur in the mid-continental distributional gap between the northeastern North American var. *michauxii* (Spreng.) Farw. [syn. subsp. *angustum* (Presl) Hultén] and the western var. *sitchense* Rupr. [syn. var. *cyclosorum* Rupr. and subsp. *cyclosorum* (Rupr.) C. Chr.] (*Fig. 2*). The distinguishing characteristics between these varieties,

as compiled from various published keys and descriptions including those of Butters (1917), Scoggan (1978, pp. 155–156), Hultén (1968, p. 48), Gleason (1952, p. 43), Fernald (1950, p. 40–41), Boivin (1967, pp. 29–30), and Hitchcock et al. (1969, pp. 63–64), are summarized in the following key:

1. Indusia more than 1 mm long, less than half as broad as long, straightish or crescent-shaped, not crossing the vein, short-ciliate; spores light brownish, smooth to sparingly papillate; pinnules more narrow, mostly 5 mm wide or less, slightly to only medium-toothed; laminae mostly less than 6 dm long, widest below the middle; stipes relatively longer, the laminae mostly less than 2(2.5) times as long as the stipes; stipe base scales 7 mm long or less, mostly dark-brown, often with blackish streaks; rhizomes horizontal to oblique-ascending, with the new frond growth appearing lateral to the tuft.....var. *michauxii*

1. Indusia mostly less than 1 mm long, about half to as broad as long, horseshoe-shaped to suborbicular, often crossing the vein, conspicuously long-ciliate; spores yellowish, more densely papillate to appearing finely warty; pinnules broader, the best-developed ones over 5 mm wide, strongly toothed or lobed to pinnatifid; laminae often more than 6 dm long, widest at or somewhat above the middle; stipes relatively shorter, the laminae mostly more than 2.5 times as long as the stipes; stipe base scales usually pale brown, mostly over 10 mm long; rhizomes strongly ascending to erect, with the new frond growth appearing central in the tuft.....var. *sitchense*

Most Saskatchewan Lady Fern collections clearly belong to the western var. *sitchense*, rather than to the eastern var. *michauxii*, despite the wider geographical gap apparently remaining to the west than to the east of the Saskatchewan populations. All the collections (including 70 individual plants) from the more western Saskatchewan regions of the Cypress Hills, Clearwater River and Lake Athabasca south shore, as well as those from the Wapawekka Hills, were consistently identifiable as var. *sitchense* (*Fig. 1*, A, B, C, and E). The collections (including 24 individual plants) from the more eastern Saskatchewan regions of Reindeer Lake–Wollaston Lake and the Pasquia Hills were also mostly determined as nearest to var. *sitchense (Fig. 1*, D and F), but at least some specimens showed various degrees of intermediacy to the eastern var. *michauxii*. The only two Saskatchewan collections to be determined as nearest to var. *michauxii* were from Courtenay Lake and from 20 km west of Numabin Bay of southern Reindeer Lake (*Ternier & Jasieniuk 1420* and *2113*, respectively).

The Lady Fern seems to display a relatively common boreal North American distributional pattern, with major eastern and western ranges of relatively high plant frequency, but an intervening central region where the plants are less common to rare and sporadic, or even absent. Our recent findings of *A. filix-femina* at widely spaced localities across Saskatchewan suggest it should be looked for as well across central and eastern Alberta and in western Manitoba. The formerly apparent mid-continental gap for the species, from western Alberta to central Manitoba, may actually be nonexistent. It is interesting that farther south across the Great Plains a similar series of "stepping stones" seems to be formed by disjunct isolates in north-central Nebraska, the Black Hills in southwestern South Dakota, and Sheridan County in northeastern Wyoming (*Fig. 2*). Most likely all of these apparently disjunct isolated populations represent relicts of a formerly continuous west–east distribution.

The author expresses his sincere appreciation to Wayne C. Harris and Sheila M. Lamont for their valuable contribution to this paper in first discovering and

collecting *A. filix-femina* in the Cypress Hills Provincial Park, and for subsequently measuring the varietally diagnostic characteristics on a standing population sample of 21 plants at the collection site. Thanks are also given to field associates, Robert A. Wright (along on all collecting expeditions), and to John H. Hudson, Donald F. Hooper, and Les Baker (each accompanying us on one field trip).

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REVIEW

HYBRIDS IN EUROPEAN ASPLENIACEAE (PTERIDOPHYTA), by T. Reichstein, Botanica Helevtica 91:89–139. 1981.—Two-thirds of the more than 30 species of European Aspleniaceae are as fully promiscuous as those of the Appalachian Asplenium complex in America, and the number of hybrids they produce is even greater. The species and their hybrids have been studied intensively since the 1950's, principally by Bouharmont, Lovis, Meyer, Reichstein, Sleep, and Vida. The present paper summarizes the accumulated knowledge of past research and presents it in the form of annotated checklists of the species and of the hydrids. Several new hybrids and new cytological results are described in two appendices, and many hybrids are illustrated with line drawings. Extensive introductory material is applicable to fern hybridization in general, as well as to European *Asplenium—D.B.L.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one more of the editors, and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of D. S. Barrington, L. E. Bishop, A. M. Evans, D. R. Farrar, F. R. Fosberg, J. D. Montgomery, R. L. Petersen, M. G. Price, H. E. Robinson, A. Sessions, A. R. Smith, and W. C. Taylor, to whom we are deeply indebted. We welcome suggestions of other reviewers.—*D.B.L.*

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ERRATA FOR 1982

Page 85, line 11 should read: "(Rousseau, 1974; Boivin, 1966; Hultén, 1958). Abbe (1936) reporting on the northern range of this species in. . ."
Page 85, line 29: For "*marina*" read "*mariana*".

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Promotion of Apogamy in Matteuccia struthiopteris, the Ostrich Fern

P. VON ADERKAS

The facultative development of sporophytes from vegetative gametophyte cells has been recorded for many species (Steil, 1939). There are also cases in which individual sporophyte organs such as sporangia develop directly on gametophytes (Lang, 1898; Lawton, 1932). The appearance of isolated organs or tissues is considered to be evidence of apomixis if the gametophytes asexually produce sporophytes (Döpp, 1967). Tracheary tissue in gametophytes of *Matteuccia struthiopteris* (L.) Todaro (Ostrich Fern) cultured over a prolonged period was not interpreted as an apogamous phenomenon, since the gametophytes did not produce buds or shoots.

Induction and promotion of apogamy in ferns has been investigated by Whittier and co-workers with an emphasis on factors such as carbohydrates (Whittier & Steeves, 1960; 1962), ethylene (Elmore & Whittier, 1975a, b), and osmotica (Whittier, 1975). These studies of *Pteridium aquilinum* have been concerned with apogamous development of buds. Attempts to induce similar development in *Matteuccia* are described in this note.

MATERIALS AND METHODS

Spores used in this study originated from a single fertile frond of a plant collected by the author (no. 821) from the Five Mile River, near South Maitland, Hants County, Nova Scotia (voucher in ACAD). Following separation from the sporangia, spores were stored in glass vials at −20°C until required. Spores were sterilized for 2 min in a solution of 3% "Clorox," a commercial bleach, to which a drop of Tween 80 surfactant had been added. Spores were trapped on a Millipore membrane filter (pore size = 8 μm) and then were washed twice with sterile, deionized water. They were plated onto Petri plates containing Knudson's medium supplemented with Nitsch's modified trace elements (Whittier, 1964), FeEDTA (1 μM), and 1% agar. These plates were placed in growth chambers set at 23°C with light level of 67 $\mu E \cdot m^{-2} \cdot s^{-1}$ and a light/dark cycle of 16:8 h. Plants were subcultured monthly, and these cultures served as stock for the experiments.

Gametophytes were incubated in Erlenmeyer flasks stoppered with silicon bungs each penetrated by a long intake and a short outlet tube. Each flask had 100 ml of Knudson's medium supplemented with varied amounts of either sucrose or sorbitol. Sorbitol is very poorly metabolized by ferns, but is preferable to mannitol which may be inhibitory to development (Hirsch, 1975). The osmolarity of the media was increased by 0, 0.06, 0.12, 0.19 osmolal, (as measured on a Fisons Osmometer Model 3W), which corresponded to concentrations of 0, 2, 4, and 6% sucrose, or 0, 1.1, 2.3, and 3.4% sorbitol.

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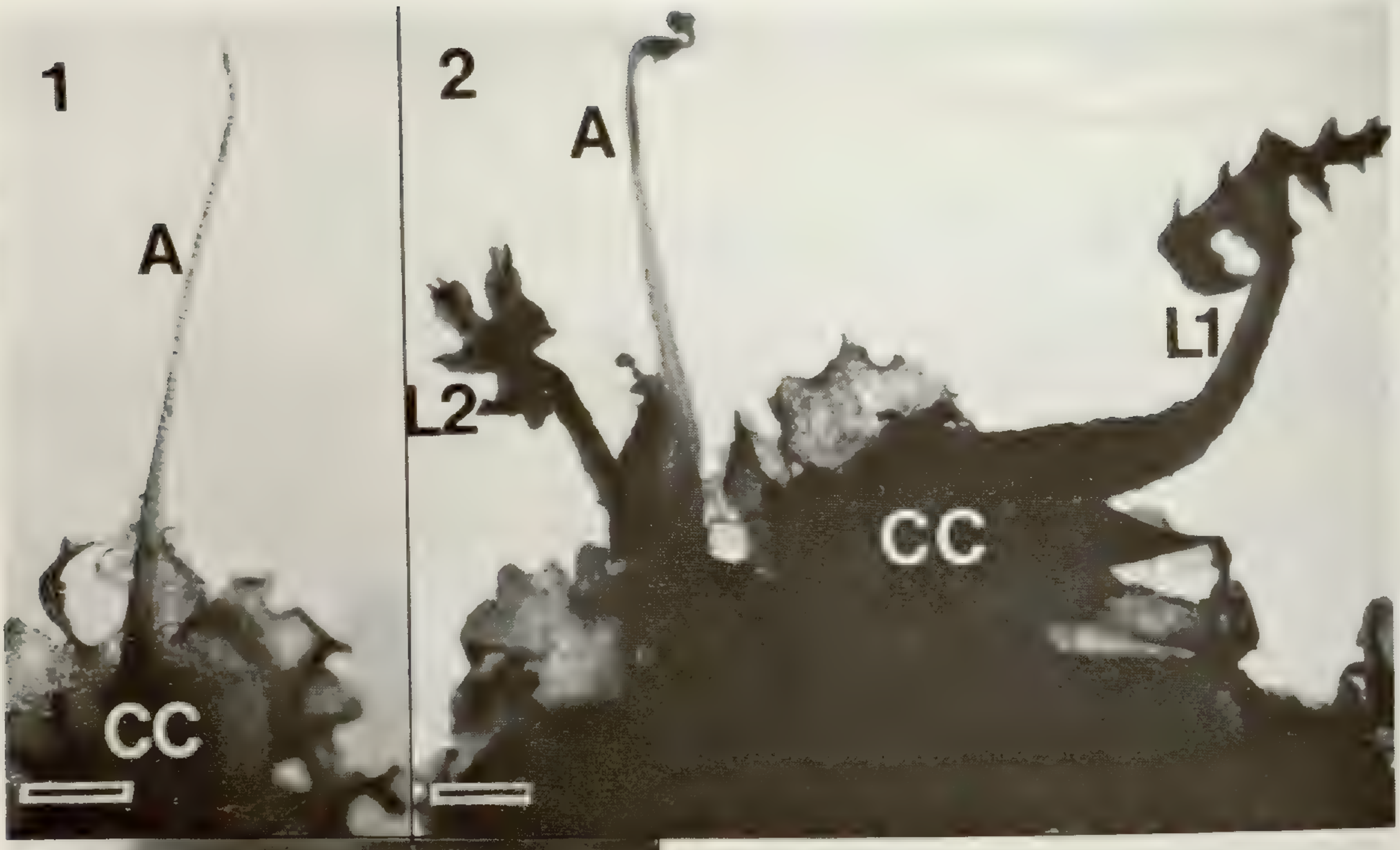
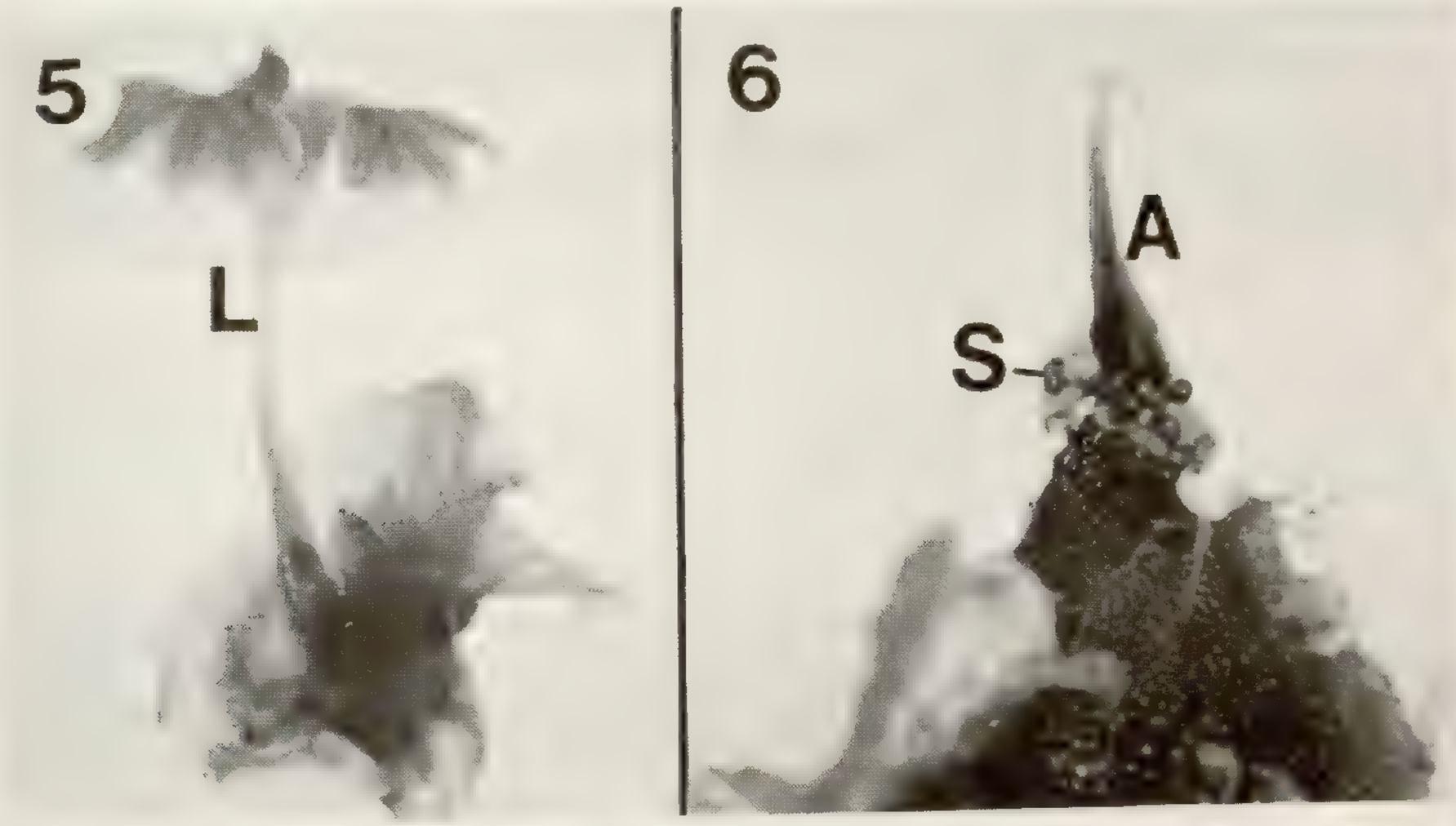


FIGS. 1–4. Sporophytic features on *Matteuccia struthiopteris* gametophytes raised in vitro. All bars = 1 mm. FIG. 1. Awl-like structure (A) arising from the anterior end of the central cushion (CC). FIG. 2. Awl-like projection from meristematic tissue and two leaves, L1 from the marginal meristem and L2 from the central cushion (CC). FIG. 3. Apogamous bud (B) surrounded by numerous glandular scales (GS). FIG. 4. Dissected juvenile leaves of apogamous sporophyte (L).



FIGS. 5–6. Sporophytic features on *Matteuccia struthiopteris* gametophytes raised in vitro. All bars = 1 mm. FIG. 5. Juvenile leaf (L) of sporophyte of sexual origin. FIG. 6. Cluster of sporangia (S) at base of awl-like structure (A).

The flasks were connected by sterilized plastic tubing (Tygon) to a glass manifold, and this assembly was linked to a 2l Erlenmeyer flask containing distilled water that served as a humidifier. One set of flasks was supplied from the central air supply, and the other from a cylinder containing 1 ppm ethylene in air (CanOx). Flow rates were maintained at 10 ml·min^{-1} with calibrated flowmeters. Gametophytes were transferred to the flasks in a laminar flow hood. The flask assembly was transferred to a growth chamber and raised under the same conditions as the stock cultures. The total weight of all plants in a replicate was recorded at the beginning of the experiment, and individual plant weights, as well as total replicate weights, were recorded at the end of a 35-day period. There were 20 plants per treatment. The experiment was run three times.

RESULTS

Structures that developed on gametophytes fell into three categories: The most frequent outgrowths were awl-like projections (91.5%) from either the marginal meristem or sub-meristematic tissue *(Figs. 1* and *2)*. Less frequent (8.3%) were reduced leaves *(Fig. 2)*, and observed only once was an apogamous bud *(Fig. 3)*. The sporophyte which developed from this bud had dissected leaves *(Fig. 4)* with an abundance of ramenta along the stipe, unlike sporophytes of sexual origin *(Fig. 5)*. There were noticeable intergradations between awl-like projections and reduced leaves, but the latter were distinguished by the obvious development of a leaf surface *(Fig. 2)*. These leaves developed from either the meristem or sub-meristematic tissue. The most extreme sporophyte reduction was a cluster of sporangia at the base of an awl *(Fig. 6)*. No spores were produced, the sporogenous tissue having aborted prior to meiosis as revealed by aceto-carmine squash of fixed material. Sporangia removed from the plant and raised on nutrient media did not develop further. Sporophytic organs were not restricted to plants of a particular size, as the smallest plants of either experiment had awl outgrowths.

TABLE 1. NUMBER OF GAMETOPHYTES (n = 60) RAISED IN DIFFERENT CONCENTRATIONS OF CARBOHYDRATE AND ETHYLENE, WHICH DEVELOPED SPOROPHYTIC STRUCTURES.

Carbohydrate	*Ethylene* (1 ppm)	
	+	−
0% sucrose	6	6
2% sucrose	37	35
4% sucrose	41	24
6% sucrose	38	35
1.1% sorbitol	30	19
2.2% sorbitol	26	20
3.3% sorbitol	27	13

TABLE 2. MEAN RELATIVE INCREASE (W_t/W_o) IN FRESH WEIGHT OF PLANTS RAISED IN DIFFERENT CONCENTRATIONS OF CARBOHYDRATE AND ETHYLENE.

Carbohydrate	*Ethylene* (1 ppm)	
	+	−
0% sucrose	2.3	2.5
2% sucrose	5.6	6.5
4% sucrose	5.3	4.5
6% sucrose	2.8	4.8
1.1% sorbitol	2.6	3.6
2.2% sorbitol	3.0	3.0
3.3% sorbitol	2.3	2.3

Apogamous development occurred most frequently on gametophytes raised on sucrose and 1 ppm ethylene *(Table 1)*. Increasing the concentration of sucrose above 2% had no effect on apogamous development. The effect of ethylene was only marginally promotive, the more pronounced effect being attributable to sucrose.

Sorbitol promoted apogamous growth compared to controls, but at a level much lower than that of parallel sucrose treatments. Sorbitol- and ethylene-treated plants had a higher frequency of apogamy than those without.

Increases in plant weight were greatest overall on media supplemented with sucrose *(Table 2)*, and these were also the treatments which elicited the highest apogamous response. However, treatment with sorbitol and ethylene elicited an apogamous response equal to that of sucrose alone, even though the former had only half the weight increase of the latter. That increase in weight of gametophyte and apogamous response are not related is made clear from the 4% and 6% sucrose treatments.

DISCUSSION

Having cultured gametophytes of *Matteuccia struthiopteris* for three years and having never observed the development of apogamous sporophytes, Mottier (1927) concluded that the "needle-like" outgrowths he had noted were not evidence of apogamy, in spite of their tracheary tissue. Döpp (1967) stated that the mere presence of a sporophytic organ or tissue on gametophytes which never asexually developed whole sporophytes was insufficient evidence of apomixis. The appearance of tracheids in gametophytes of the otherwise non-apomictic fern *Todea barbara* is a

similar case (DeMaggio, 1972). However, apogamous buds of *M. struthiopteris* do occur, and have also been isolated, albeit very infrequently, from maintained stock cultures. Apomictic sporophyte development is much less frequent in this species than in *Matteuccia orientalis* (Lloyd, 1973). Unlike some other ferns in which development of apogamous structures was preceded by formation of either a special cylindrical process (Lang, 1898) or a prothallial cushion (Whittier, 1962), in *M. struthiopteris* the reduced leaves and awls developed either directly from the marginal meristem or from tissue of the central cushion.

Promotion of apogamy has long been known to occur when a carbohydrate is added to the substrate (Whittier & Steeves, 1962). Initially, only the nutritional effects of carbohydrate were considered important (Whittier, 1964), but recently the role of osmotic potential of the media in promotion of apogamy in *Pteridium* was shown by Whittier (1975). For the Ostrich Fern there appears to be a threshold response to sucrose, but much of this sucrose effect is certainly of an osmotic nature. Similar to experiments with *Pteridium* in which an osmoticum replaced some of the requirement for sucrose (Whittier, 1975), organ development on the Ostrich Fern gametophytes occurred on up to 33% of the plants raised on sorbitol.

Nevertheless, the effects of sucrose and ethylene on apogamy differ markedly from those of a similar study on *Pteridium aquilinum* (Elmore & Whittier, 1975a). In Bracken, induction of apogamy resulted in whole plant formation, but in the Ostrich Fern, with a notable exception, only reduced sporophytic organs developed. The general failure to promote bud development in *Matteuccia struthiopteris* by the addition of compounds promotive of apogamy in *Pteridium* does not imply that the mechanisms for the two species are necessarily different. The short duration of each experiment, when compared with the 3–5 months required to induce apogamy in *Osmunda cinnamomea* (Whittier & Steeves, 1960), *Ampelopteris prolifera* (Mehra & Sulklyan, 1969) or 15 weeks for phyte formation observed.

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REVIEW

ILLUSTRATIONS OF PTERIDOPHYTES OF JAPAN, VOLUME 3, S. Kurata and T. Nakaike, eds. x + 730 pp. + folding map. 1983. University of Tokyo Press, yen 12,000.—This is the third in a continuing series of magnificent volumes with detailed treatments of 100 Japanese ferns. The third closely follows the format of the first two volumes which were reviewed in this JOURNAL 72:11. 1982 and 72:48. 1982. The unusually sturdy volumes contain line drawings, photos, and maps for each species, plus descriptions and lists of localities in Japanese. The nomenclature is as presented by T. Nakaike (Enum. Pterid. Japon. Filices, 1975) where synonymies are listed. Volume 3 is mainly devoted to *Diplazium, Polystichum* (continued from volume 1) and the thelypterids. Regrettably, the nomenclature of the thelypterids was not updated to incorporate the latest publications of Prof. R. E. Holttum. Two other minor points are that *Diplazium petri* Tard. was reduced to *D. latifrons* v.A.v.R. by Iwatsuki & Price (South East Asian Studies 14:565. 1977), and that Salisbury should not be the parenthetic author for *Thelypteris palustris* because his name was illegitimate. Furthermore, the nomenclature of the Marsh Fern in Japan, as well as in the United States, cannot be settled without a new taxonomic study. Holub (Taxon 21:331-332. 1972) believes it should be called *T. thelypteroides* (Michx.) Holub on the basis of earlier work by Morton, but Tryon and Tryon (Amer. Fern J. 63:67. 1973) are skeptical.

Fern people in North America will be especially pleased with this third volume, since it includes several other ferns besides the Marsh Fern, with which they are familiar. These are: *Polystichum braunii, P. lonchitis, P. tsus-simense* (cultivated here), *Phegopteris connectilis, Thelypteris torresiana, Cyclosorus dentatus,* and *Diplazium esculentum,* the most delicious of all ferns, with a photo showing a whole field of it.—*M. G. Price, Herbarium, North University Building, University of Michigan, Ann Arbor, MI 48109.*

A New Filmy Fern from Puerto Rico

GEORGE R. PROCTOR*

The writer is presently engaged in field work sponsored by the Puerto Rican Dept. of Natural Resources, which is intended to lead to the production of an up-to-date volume on the ferns and allied plants of this island. Already, after five months of collecting and collating other information, it appears that 45 taxa have been added to the 320 listed by Liogier & Martorell (1982), several of them new to science. At the end of one year, I intend to publish a complete checklist of Puerto Rican ferns in order to summarize new additions and describe any new species or varieties, as a preliminary to final preparation of the book.

The purpose of the present paper is partly to publicize the work being done, and partly to provide a name for a species of *Trichomanes* of which fragmentary material has already been seen from other parts of the Antilles, and which has been confused in the past with another species known only from Jamaica.

Trichomanes (Subg. Achomanes) padronii Proctor, sp. nov. **Fig. 1.**

A *Trichomanes pinnatifido* rhizomatibus crassioribus, stipitibus longioribus, laminis 6–15 cm longis pinnato-pinnatifidis, pilis ramosis vel stellatis effusioribus differt.

Rhizome wide-creeping, finely cordlike, 0.5–0.8 mm in diameter, densely clothed toward apex with flexuous, reddish, hairlike rhizoids ca. 1 mm long. Fronds distant, 9–18 cm long, long-stipitate; stipes 3–4.5 cm long, shorter than the blades, nonalate except at the extreme apex, loosely and deciduously clothed with branched or stellate, pluricellular hairs up to 1.3 mm long; similar hairs also on vascular parts and margins of the blade. Blades oblong-lanceolate, 6–15 cm long, 2.5–3.5(5) cm broad, pinnate-pinnatifid, acuminate at the apex, subtruncate at the base; rhachis alate (wings 0.3–0.7 mm wide on either side); pinnae ascending, alternate, 7–13 on a side below the pinnatifid apex, 1.5–2.5 cm long, short-stalked (the stalks winged like the rhachis), the expanded portion rhombic-acuminate, 1–1.5 cm broad below the middle, deeply pinnatifid, the segments oblique, the largest ones narrowly oblong, obtuse, with lobed margins; costules of basal segments arising oppositely from costa, in turn with opposite or subopposite simple branches, each vein extending to the apex of a lobe. Sori numerous, apical on the lobes or smaller segments; involucres immersed, oblong-turbinate or turbinate, 1.7–2 mm long, the apex subtruncate to slightly flaring; receptacle becoming long-exserted.

TYPE: South of Road 120 ca. 0.5 km ESE of Observation Tower, Maricao State Forest, Município San Germán, Puerto Rico, elev. 850–860 m, 23 November 1983, *G. R. Proctor 39833* (US). Scandent on trunk of a tree-fern in subtropical wet forest, serpentine substrate.

Collected with, and named for, Sr. Rubén Padrón, diligent and well-informed Biologist in Charge of the Maricao State Forest.

This species has been recorded from Hispaniola under the name *Trichomanes pinnatifidum* v. d. Bosch (Christensen, 1937, p. 10), but that species as now understood is endemic to Jamaica. *Trichomanes padronii* clearly differs from *T. pinnatifidum* in its thicker, more robust rhizome, larger and more divided fronds with much longer stipes, longer and more loosely-spreading hairs, and differently

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FIG. 1. Portion of holotype of *Trichomanes padronii* (Proctor 39833, US).

located sori. A peculiar feature exists in the branching pattern of *T. padronii*, which is neither clearly anadromous (as in subg. *Trichomanes* and *Pachychaetum*) nor catadromous (as is usually the case in subg. *Achomanes*). In fact, the basal divisions of the pinnae are almost exactly opposite, as are many of the ultimate veins arising from the costules of the segments. The species is assigned to subg. *Achomanes* because of the branched and stellate marginal hairs.

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Chromosome Numbers of Neotropical Isoëtes

R. JAMES HICKEY*

Chromosome counts have been made for a number of *Isoëtes* found in eastern North America, Europe, and India. Typically the haploid complement of $n=11$, or a multiple thereof, has been reported (Löve et al., 1977; Kott & Britton, 1980). Polyploid series range from $2n=22$ to $2n=110$. The aneuploid *I. durieui* is notable in having the lowest chromosome number in the genus, with $2n=20$. Several taxa from India, including *I. coromandelina* Linn. f., *I. panchananii* Pant & Srivastava, *I. indica* L. Rao, and *I. pantii* Goswami & Arya, are reported to possess one or two supernumerary chromosomes (Goswami, 1975; Pant & Srivastava, 1965). Only *Stylites gemmifera* Rauh [=*Isoëtes andicola* (Amstutz) L. D. Gómez] shows a strong deviation from the presumed base number of $x=11$. According to Rauh and Falk (1959), the diploid number for this species is ca. 58.

Mexico, Central America, the Antilles, and tropical South America, with over fifty taxa, are exceptionally rich in *Isoëtes*. In addition, the morphological diversity in these taxa is perhaps greater than in any other part of the world. Among the neotropical species, only the count for *I. andicola* has been reported (Rauh & Falk, 1959). As part of an overall systematic revision of the Neotropical *Isoëtes*, the chromosome numbers of several species were studied and are reported here. Some of these counts have been previously mentioned in Tryon & Tryon (1982), at which time I ascribed a count of $2n=44$ in *I. ticlioënsis* H. P. Fuchs *nom. nud.* to *I. lechleri* Mett.

METHODS AND MATERIALS

The specimens of neotropical *Isoëtes* examined in this study were grown in the alpine greenhouse of the Biological Sciences Group at The University of Connecticut. All taxa, with the exception of *I. andicola*, were cultivated fully submerged in glass aquaria in the Alpine Room under ambient day length. Specimens of *I. andicola* were potted in rich humus constantly saturated from beneath and kept at 4°C in a cold room under a 16 hour day length. Voucher specimens are deposited in the Gray Herbarium, Harvard University (GH), and duplicates are in the author's herbarium.

To obtain roots for cytological study, corms were rinsed in water and all roots removed; the plants were then grown as floating aquatics until new roots emerged from the fossae. The roots were harvested when 1–2 cm long and were soaked for 4–6 hours in a saturated solution of paradichlorobenzene at room temperature. Roots were harvested in the morning, as suggested by Kott and Britton (1980). Following pretreatment, the roots were blotted dry and fixed in Farmer's Solution for a minimum of 24 hours. The roots were hydrolyzed in hot 1N HCl for 30 minutes, deacidified in 95% ethanol, and stained with Whittman's hematoxylin. The root tips were then destained in glacial acetic acid and squashed in Hoyer's medium (Willey, 1971).

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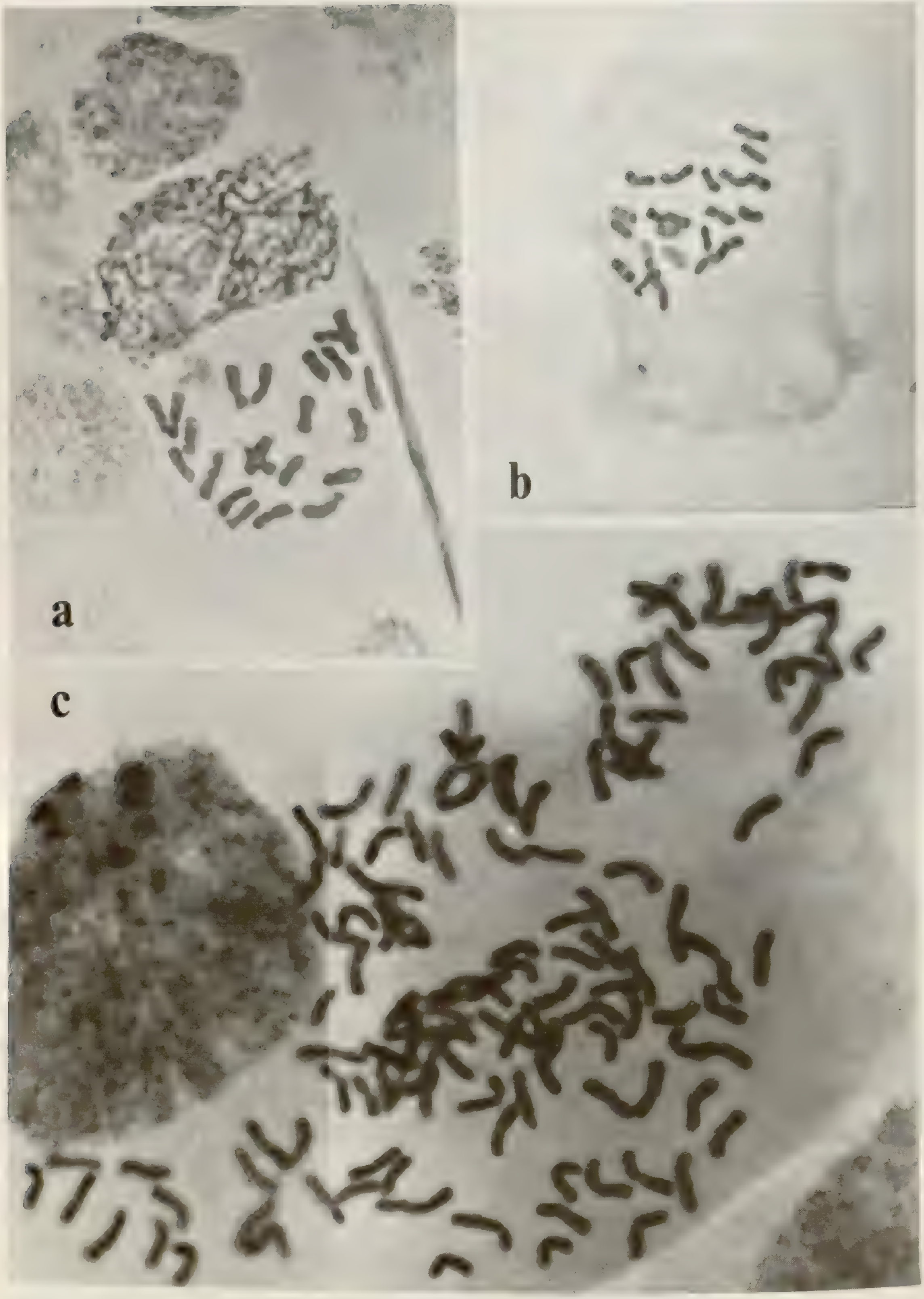

FIG. 1. Diploid and dodecaploid species of *Isoëtes*, ×1500. a. *Isoëtes storkii*, $2n = 22$. b. *Isoëtes alcalophila*, $2n = 22$. c. Composite photo of *I. novo-granadensis*, $2n = 132$.

TABLE 1. NEW CHROMOSOME COUNTS OF NEOTROPICAL *ISOËTES*

Isoëtes alcalophila Halloy
  $2n=22$: Argentina: Prov. Tucumán, Laguna Muerta, October 1980, *Halloy s.n. (Fig. 1b).*
Isoëtes andicola (Amstutz) L. D. Gómez
  $2n=44$: Peru; Dept. Junín, Lago Junín, April 1979, *Karrfalt s.n. (Fig. 2c).*
  $2n=44$: Bolivia; Prov. Bautista Saavedra, *Feuerer 5948*
Isoëtes boliviensis U. Weber
  $2n=22$: Bolivia; Prov. Omasuyos, *Hickey 753 & Eshbaugh*
Isoëtes glacialis Asplund
  $2n=44$: Bolivia; Prov. Murillo, *Hickey 839 & Eshbaugh (Fig. 2b).*
Isoëtes herzogii U. Weber
  $2n=44$: Bolivia; Dept. Cochabamba, *Hickey 819 & Eshbaugh (Fig. 2a).*
  $2n=44$: Bolivia; Dept. Cochabamba, *Hickey 821 & Eshbaugh*
Isoëtes novo-granadensis H. P. Fuchs
  $2n=132$: Ecuador; Prov. Napo, *Sperling, Øllgard & Roth 5189 (Fig. 1c).*
Isoëtes storkii T. C. Palmer
  $2n=22$: Costa Rica; Prov. Alajuela, Volcán Poás, *Churchill 3284 (Fig. 1a).*
  $2n=22$: Costa Rica; Cerro de La Muerte, *Anderson 1439*
Isoëtes ticlioënsis H. P. Fuchs, *nom. nud.*
  $2n=44$: Peru; Dept. Lima, Ticlio Pass, *Hickey 840 & Eshbaugh*
  $2n=44$: Peru; Dept. Lima, Ticlio Pass, *Hickey 842 & Eshbaugh (Fig. 2d).*

Slides were examined with a Zeiss research microscope under bright field and phase contrast. Photographs were taken using Kodak High-Contrast film.

RESULTS AND DISCUSSION

The recently described *I. alcalophila* Halloy (Halloy, 1979) from Argentina, *I. boliviensis* U. Weber from Bolivia, and the Costa Rican *I. storkii* T. C. Palmer are diploids, $2n=22$ *(Fig. 1a, b, Table 1). Isoëtes glacialis* Asplund, *I. herzogii* U. Weber, and the undescribed *I. ticlioënsis* of H. P. Fuchs (Fuchs-Eckert, 1982), are tetraploids with $2n=44$ *(Fig. 2).*

In 1980, L. D. Gómez transferred *Stylites andicola* Amstutz, the type of *Stylites*, into *Isoëtes*, and recognized the gemmiferous plants as *I. andicola* var. *gemmifera* (Rauh) L. D. Gómez. After studying several gemmiferous species in the field, and over 200 individuals of *I. andicola* from throughout its range, I think that gemmae production is facultative, and so *I. andicola* should be considered a monotypic species. Eight chromosome counts from both gemmiferous plantlets (Karrfalt material) and young, non-gemmiferous plants (Feuerer material) yielded a diploid number of 44. The discrepancy between these counts and the previous report of $2n=$ca. 58 (Rauh & Falk, 1959) may well be the result of chromosome fragmentation, which I have found to be a common occurrence in many neotropical species. However, the possibility of a cytologically distinct population cannot be ruled out. My counts provide additional support for the inclusion of *Stylites* in *Isoëtes*.

Two cells of *I. novo-granadensis* have yielded counts of 132 *(Fig. 1c)*, and several others have yielded counts of 126, 128, and 129. The dodecaploid *I. novo-granadensis* has the highest chromosome count yet recorded for the genus. The previous high, $2n=110$, had been recorded for *I. lacustris* (Löve et al., 1977; Kott & Britton, 1980) and *I. macrospora* (Kott & Britton, 1980).

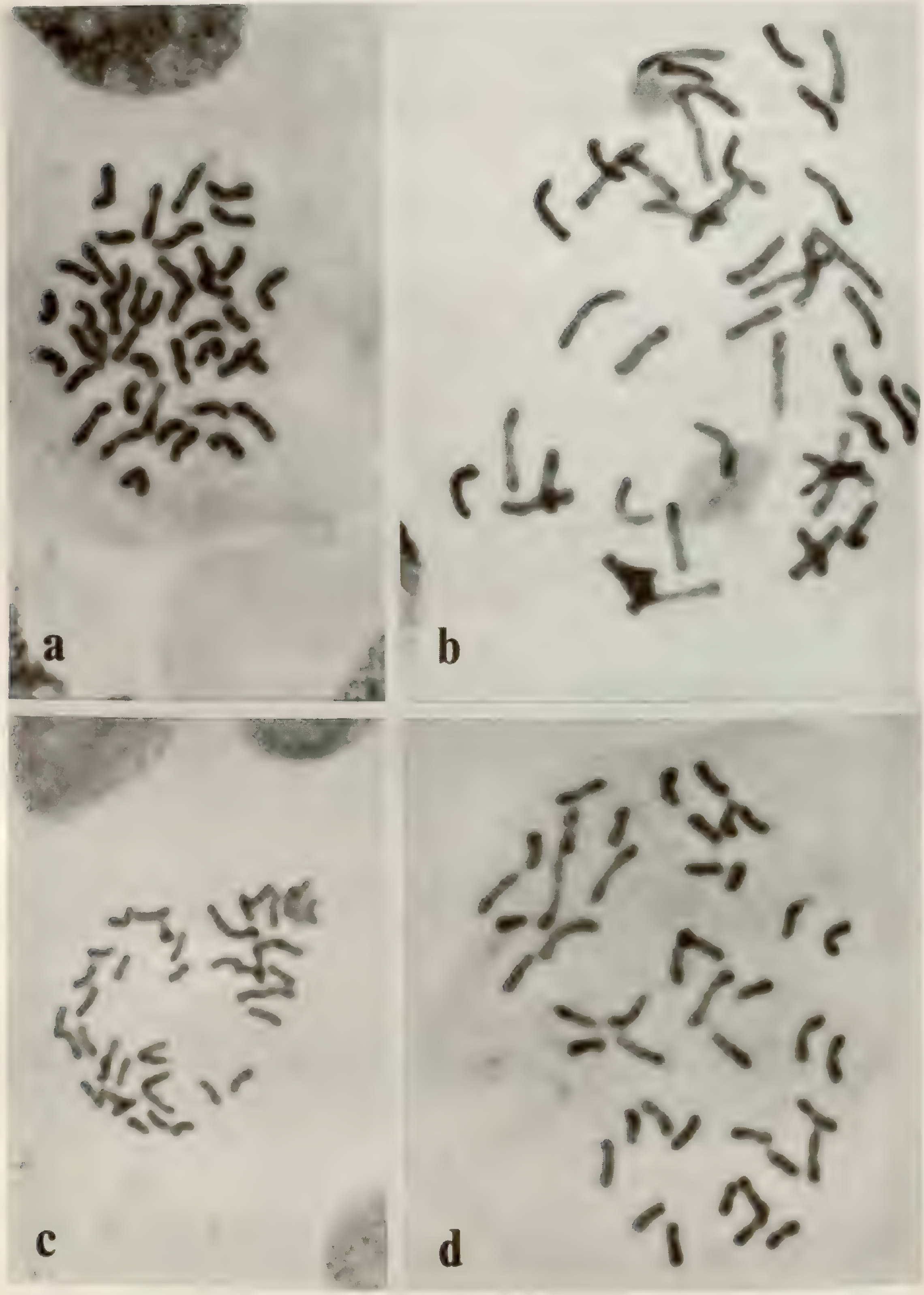

FIG. 2. Tetraploid species of *Isoëtes*, ×1500. a. *Isoëtes herzogii*, $2n=44$. b. *Isoëtes glacialis*, $2n=44$. c. *Isoëtes andicola*, $2n=44$. d. *Isoëtes ticlioensis*, $2n=44$.

The use of chromosome numbers and other cytological data promises to be of considerable significance in understanding the evolution of *Isoëtes* species. The large size and variable morphology of the chromosomes (e.g., secondary constrictions, satellite DNA) in the neotropical species suggest that karyotype analysis might lead to a better understanding of the evolutionary history of the genus. For example, karyotype analysis has proven useful in the elucidation of triploid derived *Isoëtes* aneuploids ($2n = 33 + 1$) in India (Kuriachan & Ninan, 1974). Such investigations are particularly needed in *Isoëtes*, where morphological characters are notoriously plastic.

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Two New Phenolic Glycosides in Asplenium septentrionale

FILIPPO IMPERATO*

On the basis of data from morphological and cytological analyses, Wagner (1954) suggested the concept of reticulate evolution in the Appalachian *Asplenium* complex, which was subsequently confirmed by Smith and Levin (1963) using chemical analysis. It is interesting to note in this regard that the morphological characteristics of the hybrids are generally intermediate between their parents, but that the chemical constituents of the hybrids show a total addition of parental attributes; Appalachian *Asplenium* plants clearly demonstrate additive inheritance of chemical characters. Recently it has been shown that the chemistry of European *Asplenium adiantum-nigrum* complex is analogous to that of Appalachian *Asplenium* complex (Richardson & Lorenz-Liburnau, 1982). In spite of the foregoing studies, the chemistry of most species of *Asplenium* is not well known.

In the present investigation, a new kaempferol tetraglucoside (I) and a new sulphate ester of 1-p-coumarylglucose (II) have been isolated from the fronds of *A. septentrionale;* moreover two other sulphate esters of hydroxycinnamic acid-sugar derivatives (III and IV) have been found in this plant material.

Previous work on the chemical constituents of *A. septentrionale* has led to the identification of amino-acids (4-hydroxy-4-methylglutamic acid, 2-amino-4-hydroxy-pimelic acid and the corresponding lactone, N-acetylornithine) by Berti and Bottari (1968), keto acids (pyruvic, hydroxypyruvic, 2-oxoglutaric, 2-oxopimelic, and 4-hydroxy-2-oxo-pimelic acids) by Virtanen and Alfthan (1954), and cyanogenic glucosides by Hegnauer (1961). Very recently Imperato (1983) reported isoquercitrin and a new flavonoid (quercetin 3-0-(3″-sulphate) glucoside) from *A. septentrionale*.

MATERIALS AND METHODS

An *A. septentrionale* plant was collected on Mt. Etna, Italy. Fresh fronds were homogenized and extracted with hot 95% ethanol. The extracts were concentrated to a small volume in a vacuum and were filtered. Phenolic glycosides were isolated by preparative paper chromatography on Whatman 3MM paper in n-butanol-acetic acid-water (4:1:5, upper phase). The bands, revealed under ultraviolet light with ammonia vapor, were cut off, eluted with 70% ethanol, concentrated, and rechromatographed in 15% acetic acid and in n-butanol-ethanol-water (4:1:2,2).

Total acid hydrolysis of isolated phenolic glycosides was carried out with 2N HCl (1 hr at 100°C); controlled acid hydrolysis was carried out with 10% acetic acid (3.5 hr under reflux). Enzyme hydrolysis with ß-glucosidase was carried out in citrate-phosphate buffer (pH 4.5 at 37°C for 20 hr). The aglycone:sugar ratio was determined according to Nordström and Swain (1953). Aglycones were identified by ultraviolet spectral analysis with the customary shift reagents (Mabry et al., 1970), paper co-chromatography with authentic samples (four solvent mixtures) and polyamide TLC. Sugars were identified by paper co-chromatography (three solvent mixtures) and SiO_2 TLC. Sulphate was identified using barium chloride. Flavonol

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SPECTRAL PROPERTIES AND R_f VALUES OF KAEMPFEROL 3-SOPHOROTRIOSIDE-7-GLUCOSIDE

Spectral properties		*R_f values*	
Shift reagent	MeOH λ_{max}	*Solvent mixture*	R_f (×100)
—	265,352	BAW	33
NaOAc	263,375	BEW	48
$NaOAc/H_3BO_3$	260,340	H_2O	90
$AlCl_3$	274,297,343,385	15% HOAc	74
$AlCl_3$/HCl	272,300,339,385	PhOH	51
NaOMe	273,385 (inc)		
$ZrOCl_2$/citric acid	263,332		

BAW = n-butanol-acetic acid-water (4:1:5, upper phase), BEW = n-butanol-ethanol-water (4:1:2,2), PhOH = phenol saturated with water, inc = shift accompanied by increase in intensity.

glycosides obtained by controlled acid hydrolysis and by enzyme hydrolysis were identified by paper co-chromatography with authentic samples (four solvent mixtures), by ultraviolet spectral analysis with the customary shift reagents (Mabry et al, 1970) and by acid hydrolysis. Phenolic glycosides were methylated with methyl iodide in dimethylformamide in the presence of silver oxide (18 hr in the dark at room temperature under stirring), and the permethylated products were hydrolysed by refluxing for 4 hr with 0.3 N HCl. Methylated sugars were identified by paper co-chromatography with authentic samples (Petek, 1965) and SiO_2 TLC; the partially methylated aglycones were identified by paper co-chromatography and UV spectroscopy.

RESULTS AND DISCUSSION

Color reactions (brown to yellow in ultraviolet + NH_3), R_f values and ultraviolet spectral characteristics (see *Table 1*) of the isolated flavonoid (I) were consistent (Mabry et al., 1970) with those of a 3,7-disubstituted flavonol glycoside with free phenolic hydroxyl groups at positions 5 and 4′. Total acid hydrolysis gave kaempferol and D-glucose; quantitative examination gave an aglycone:sugar ratio of 1:4.1. Controlled acid hydrolysis gave kaempferol, kaempferol 7-O-glucoside, D-glucose, sophorose (2-O-ß-glucosylglucose) in small quantities, and a sugar which on paper chromatography behaved as a trisaccharide. This sugar, isolated by preparative scale chromatograms, gave glucose by total acid hydrolysis, whereas by controlled acid hydrolysis it gave glucose and sophorose; these data are consistent with this trisaccharide being sophorotriose (O-ß-glucosyl-(1 2)-O-ß-glucosyl-(1 2)-glucose). Moreover, since this sugar was obtained from flavonoid (I) by H_2O_2 oxidation (Chandler & Harper, 1961), it must be linked to the 3-hydroxyl group of kaempferol. On enzyme hydrolysis with ß-glucosidase, (I) gave D-glucose, kaempferol 3-O-sophorotrioside, and kaempferol in very small quantities. Methylation of (I) followed by acid hydrolysis gave 2,3,4,6-tetra-O-methyl-D-glucose, 3,4,6-tri-O-methyl-D-glucose, and kaempferol 5,4′-dimethyl ether. These results show that the isolated flavonol tetraglucoside (I) must be kaempferol-3-O-sophorotrioside-7-O-glucoside, which is a new natural product *(Fig. 1)*.

Flavonol 3,7-diglucosides have already been found in two *Asplenium* species, *A. rhizophyllum* (Harborne et al., 1973) and *A. trichomanes* (Imperato, 1979). From the

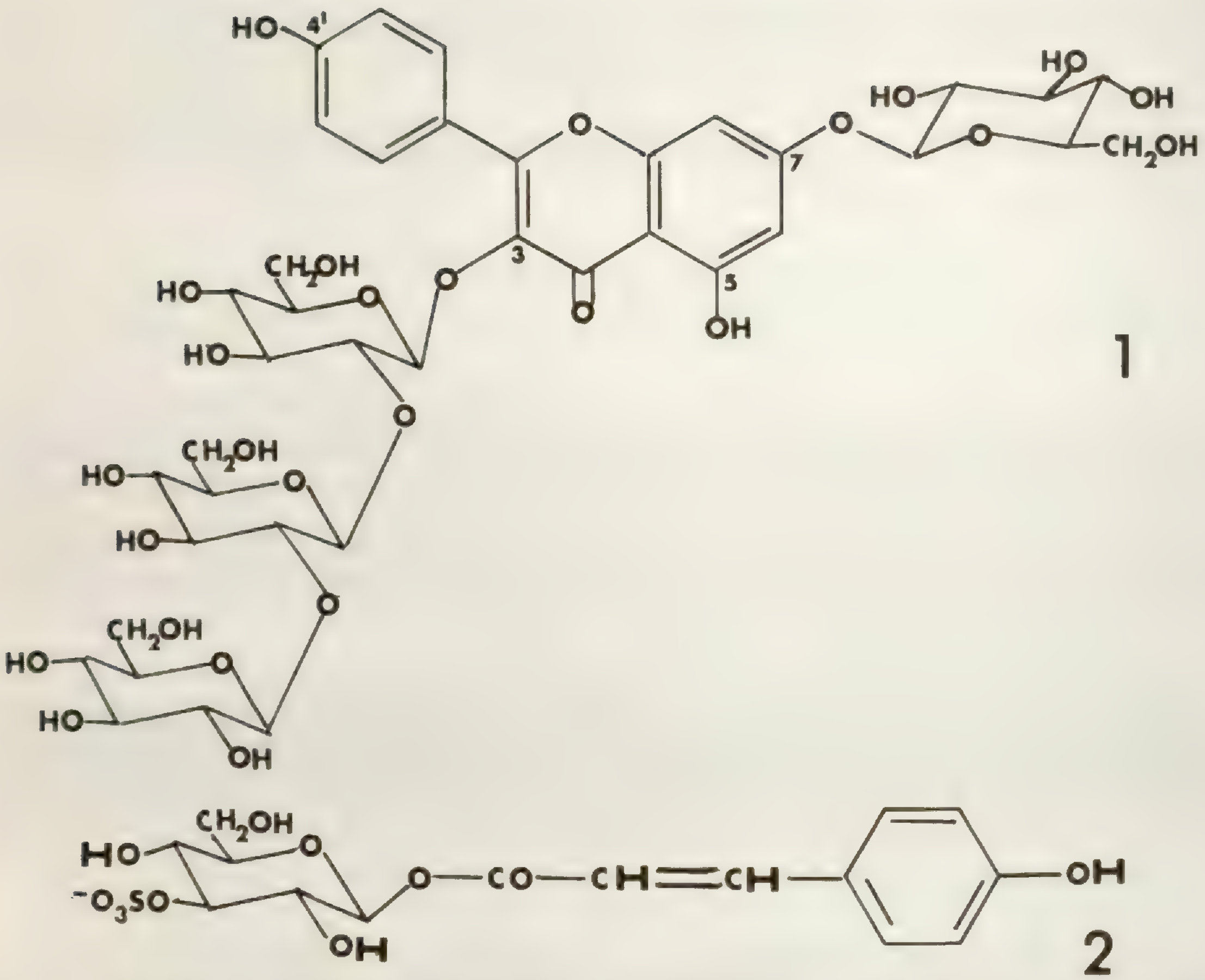

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FIG. 1. Structural formula of compound (I), kaempferol-3-O-sophorotrioside-7-O-glucoside.
FIG. 2. Structural formula of compound (II), 1-p-coumarylglucose 3″-sulphate.

systematic viewpoint, this is of interest because it has been suggested (Harborne, 1965) that flavonol 3,7-diglycosides are of restricted distribution.

Of the three hydroxycinnamic acid-sugar derivatives isolated from *A. septentrionale*, compound (II) has been proved to be a new natural product in the following way. The compound (color reactions: colorless to blue in ultraviolet + NH_3) was electrophoretically highly mobile (toward the anode) and strongly suggestive of a sulphate derivative. On both total acid hydrolysis and controlled acid hydrolysis, p-coumaric acid, D-glucose, and sulphate were obtained. Since the ultraviolet spectrum (λ_{max}^{MeOH} 312 nm) showed a large bathochromic shift (50 nm) in the presence of NaOMe, the phenolic hydroxyl group of p-coumaric acid must be free (Harborne & Corner, 1961). Methylation followed by acid hydrolysis gave p-methoxycinnamic acid and 2,4,6-tri-O-methyl-D-glucose. These results show that compound (II) must be 1-p-coumarylglucose 3″-sulphate, which is a new natural product *(Fig. 2)*.

The two remaining phenolic glycosides (III and IV) isolated from *A. septentrionale* have been characterized as sulphate esters of 1-p-coumarylglucose by the above methods, but the position of sulphation on the glucose has not been determined because these products could not be obtained in sufficient amount for their characterization to be completed.

Sulphate esters of hydroxycinnamic acid-sugar derivatives were reported for the first time by Cooper-Driver and Swain (1975), who found sulphate esters of p-coumaryl- and caffeylglucose in *Pteridium aquilinum* and in ten *Adiantum* species. Subsequently, the following compounds have been isolated from ferns: 2-O-p-coumarylglucose 6-sulphate from *Asplenium fontanum* var. *obovatum* (Imperato, 1981), 2- and 3-sulphates of 1-caffeylglucose from *Ceterach officinarum* (Imperato, 1981), and 1-p-coumarylglucose 2-sulphate and 1-caffeylgalactose 6-sulphate from *Adiantum capillus-veneris* (Imperato, 1982). Although sulphate esters of hydroxycinnamic acid-sugar derivatives have been found mainly in ferns, they have been isolated also from higher plants, e.g., from the grass *Paspalum convexum* (Harborne, 1977).

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REVIEW

A MONOGRAPH OF THE FERN GENUS PLATYCERIUM (POLYPODIACEAE), by E. Hennipman and M. C. Roos. 1982. North Holland Publishing Company, Amsterdam and Oxford, New York. $63.00.—This little 124-page book on the staghorn ferns, *Platycerium,* is attractively presented on glossy paper with numerous figures and plates, some of the latter in color. No cultivated ferns are more spectacular than these showy plants, so familiar in conservatories the world around. The book is divided into two sections: general and taxonomic. The former contains the taxonomic history, habitats, morphology, phylogeny, generic relationships, species concepts, and geography. Notable is the detailed character analysis for primitive and divergent states, which emphasizes leaf structure and trichomes, including scales, hairs, and paraphyses. The phylogeny is constructed according to the sister group method, but the resulting graph, unfortunately, is so complicated, the actual lines partially obscured by character bars that are too wide, that it resembles a damaged Venetian blind. Character 18 (frond structure) is practically chaotic, as are some of the other divergent, multistate characters in which the separate trends have not been sifted out. On the other hand, the geographical analysis is especially interesting and well done.

The taxonomic section contains the generic description, keys, descriptions, and range maps. The authors base their taxonomic conclusions on studies of dried materials from 22 herbaria and living plants in seven botanical gardens. They reduce the number of species from the 18 recognized by Barbara Joe Hoshizaki to 15 by treating several of her species as infraspecific taxa. All characters considered, *Platycerium stemaria* appears to be the most primitive of the present-day species, being closest to the groundplan by having the least number of divergences. In the taxonomic treatment, I was disappointed to see the taxa arranged alphabetically rather than according to clusters of relationship worked out in the construction of monophyletic groups. I agree with the authors that it is not necessary to name the groups formally. The end of this fine book contains not only an index of collections, but also valuable notes on collecting and preparing specimens of these ferns. All in all this is a splendid contribution to pteridology, and I strongly recommend it to all students of ferns, including fern horticulturists. The authors are to be congratulated. —*W. H. Wagner, Jr., Department of Botany, University of Michigan, Ann Arbor, MI 48109.*

A Remarkable Cyathea Hybrid

R. E. HOLTTUM*

I recently discovered, in the Herbarium at Kew, specimens of a hybrid *Cyathea* plant cultivated at the Birmingham, England Botanical Gardens in 1890 and of the two plants stated to have been parents of the hybrid. The specimens were sent to Kew by W. B. Latham, who was Curator of the Birmingham Gardens from 1868 to 1903. The only published reference to the hybrid known to me is in an account of his career by Latham (1901), in which he stated that he raised the hybrid about 1870 and that the parent species were "the Mexican *Cyathea insignis* and the Norfolk Island *Alsophila excelsa*"; he did not give a distinctive name to the hybrid. He also referred to a *Dicksonia* hybrid which he raised in 1862 and which was named *D. lathamii* by Thomas Moore (1885).[1] Thus Latham was a pioneer in fern hybridizing, although he is not mentioned in the book by E. J. Lowe on the subject. Lowe (1895, p. 11) recorded that when he began experiments in 1851, Thomas Moore and others told him that hybridization of ferns was impossible; for comments on Lowe's work as recorded in his book, see Lovis (1967).

Although Latham accepted the nomenclature which placed in different genera the parent plants of his *Cyathea* hybrid, he evidently recognized their close relationship. They both belong to *Cyathea* subg. *Sphaeropteris* in my arrangement of Cyatheaceae of the Old World (Holttum, 1963, 1964), where about 100 species of the subgenus are recognized.

In 1970, R. M. Tryon recognized *Sphaeropteris* as a distinct genus, including in it not only the American species mentioned by me (1963, p. 124), but also several others which in my judgement are quite unrelated. The six American species which I regard as true *Sphaeropteris* were described by Tryon (1971) as "the group of *Sphaeropteris horrida*." In this group, two species are closely allied; they are named by Tryon *S. insignis* (D. C. Eaton) Tryon (from the Greater Antilles) and *S. horrida* (Liebm.) Tryon (from southern Mexico). Baker (1874, p. 17) united the two as *Cyathea insignis* D. C. Eaton, but in cultivation the Mexican species became known as *C. princeps* E. Mayer, and Latham so named the specimen of the Mexican parent of his hybrid; see Tryon (1971) for a full synonymy. Latham's specimen is sterile, but its scales indicate that it belongs either to *S. insignis* or to *S. horrida*, as named by Tryon. Latham said that it came from Mexico, and by comparison with specimens in the Kew herbarium I judge that he was right. The specimen certainly does not belong to any Old World indusiate species of subg. *Sphaeropteris*.

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[1]Latham claimed that this was a hybrid between *D. arborescens* L'Hérit. from St. Helena and *D. antarctica* Labill. of Australia. The habit of the plant as described by Latham, and specimens sent by him to Kew, indicate that it is intermediate between the alleged parents in various ways. The original plant, now 120 years old, is still alive (its height was lowered by air-layering about 1950), and some experimental work on it is now in progress; I hope a report on it will appear in due course.

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Latham's specimen of the other parent shows clearly that it belongs to the species from Norfolk Island originally named *Alsophila excelsa* R. Brown. When transferred to *Cyathea*, the name must be changed to *C. brownii* Domin because there is a different species named *C. excelsa*.

Thus there is no doubt that Latham's two parent plants came from countries about 10,000 km apart. His hybrid is certainly intermediate in its characters of indusia and scales; I therefore regard his claim as justified, and name his hybrid as follows:

Cyathea (Sphaeropteris) ×lathamii Holttum, hybr. nov.

Inter *C. princepem* E. Mayer (Gartenflora 17:10. 1868) et *C. brownii* Domin (Pteridophyta 262. 1929); a *C. principe* differt indusiis rudimentariis ambitu irregulari, squamulis costarum pinnularum brevioribus; a *C. brownii* differt soris indusiis rudimentariis, non squamulis discretis, cinctis, squamulis costarum pinnularum majoribus, setis multis castaneis instructis.

TYPE: Cultivated in the Birmingham Botanical Gardens, England, 9 July 1890, *W. B. Latham* (K).

In *C. princeps* the indusia are quite large, opaque, and of a firmer texture than those of all other species of the subgenus except *C. insignis*. They completely cover the young sori, but at maturity develop an apical aperture to form cups with contracted rims; these cups soon develop two or three splits to the base (Tryon, 1971, figs. 7, 8). In *C. brownii* there are no indusia; each sorus is surrounded by several narrow scales, as in most exindusiate species of the subgenus. In the hybrid the base of the receptacle is surrounded by a continuous disc of irregular size and very uneven outline.

The costal scales in *C. princeps* are commonly 5 mm long and nearly all have firm, brown, marginal setae; the larger scales are wholly brown, whereas some others are colorless but firm. In *C. brownii* the costal scales rarely exceed 1 mm long and nearly all are thin and pallid with short, pallid, marginal hairs. The scales of the hybrid are about 1.5 mm long and nearly all have firm, brown setae.

Schneider (1892, p. 354; 1893, p. 83) gave a contemporary report on the cultivation of the parent species in Britain. His comment on *C. brownii* is that young plants grow very quickly and are "every year sacrificed in enormous quantities for indoor decoration." His comment on *C. insignis* indicates that plants so named were then well known in cultivation in English greenhouses; he did not distinguish between *C. insignis* and *C. princeps*.

Among other specimens at Kew made from cultivated plants of *Cyathea* is one labelled "Madeira (cult.), comm. C. L. Power, 25 April 1904." All sori are old and all show indusia comparable with those of Latham's hybrid, although most are somewhat larger. The costal scales are small, mostly pallid but with rather long, marginal setae, colored or not. The pinnule lobes are very firm and rather deeply lobulate, not evidently glaucous. I suggest that this represents another hybrid within subg. *Sphaeropteris*, one parent being possibly *C. cooperi* (F. v. Muell.) Domin of Queensland, which has become widely distributed in cultivation (some years ago it was a weed in the fern houses at Kew).

I know of no other records of fern hybrids the parents of which are so widely separated geographically as those of *C. ×lathamii*, but it is notable that such have

been produced in angiosperms (e.g., *Eucryphia* ×*intermedia* Bausch, the parents of which are *E. glutinosa* from Chile and *E. lucida* from Tasmania).

So far as I know, no other hybrids, either wild or cultivated, have been reported between species of *Cyathea* subg. *Sphaeropteris* sect. *Sphaeropteris* Holttum (1963). However, in sect. *Schizocaena* there is a probable wild hybrid between *C. moluccana* R. Br. in Desv. (simply pinnate and indusiate) and *C. squamulata* (Blume) Copel.; it is named *C. alternans* (Wall. ex Hook.) Presl (Holttum, 1963, p. 145).

The existence of Latham's hybrid is one more piece of evidence that in *Cyathea sensu* Holttum (1963) species with indusia and species lacking indusia may be related genetically. In his account of the genus *Cyathea*, as restricted by him, Tryon (1976) described five putative hybrids between indusiate species which he includes in *Cyathea* and exindusiate ones which he includes in *Trichopteris*. Tryon (1970, p. 15) separated these genera solely on the presence or absence of indusia; this separation seems to me unnatural. In Holttum and Edwards (1983, pp. 163–164) I suggested that *Cyathea*, *Trichopteris*, and part of *Sphaeropteris sensu* Tryon (1970) need to be united and resubdivided in a new way; such a subdivision presents very complex problems. Experimental hybridization might offer clues to their solution. As Tryon remarked (1970, p. 42), hybrids between two indusiate, or two exindusiate, species are difficult to detect from herbarium specimens and may be more abundant than is at present apparent.

The problem of the origin of the American species of subg. *Sphaeropteris* remains uncertain. As the subgenus is very much more diverse in the Old World (ca. 100 species, with rather distinct divisions named *Schizocaena* and *Fourniera*) than in the New World, an origin in southeastern Asia is surely indicated. Tryon (1971, p. 7) wrote "*Sphaeropteris insignis* and *S. horrida [Cyathea princeps]* may be considered as the most primitive species in the [tropical American] group on the basis of their open indusia and their crozier scales which bear wholly antrorse teeth." But as no Old World species has such indusia, I suggest that the condition is more likely to be a local development, also the antrorse setae on the stipe scales of the other species.

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The Ligule In Isoëtes

B. D. SHARMA and R. SINGH*

The ligule was first illustrated in *Lepidodendron* by Solms-Laubach (1892). Williamson (1894) described its structure under the name "adenoid organ." Maslen (1898) found the ligule to be a small triangular point in *Lepidostrobus,* while Seward (1910) described the occurrence of "ligule pits" in the leaf bases of *Lepidodendron* and *Lepidophlois*. Scott (1920) suggested size variation in the ligule, from a small, pointed body as in *Lepidostrobus* to an elaborate structure, e.g. in *Miadesmia.* Recently Grierson and Bonamo (1979) described the presence of a ligule in the Middle Devonian species *Leclercquia complexa.* Among the living representatives of lycopods, this structure exists in *Selaginella, Isoëtes,* and *Stylites;* on this basis these genera are sometimes grouped together as the "Ligulatae" (Sporne, 1975).

A number of functions have been assigned to the ligule. It is believed to be a secretory or nutritive organ, or both, which by exuding water and mucilage serves to keep the young leaves and sporangia moist (Foster & Gifford, 1959; Bierhorst, 1971; Sporne, 1976). Michaux (1973) studied the ultrastructure of the cells of the ligule and found that the mucilagenous secretion possessed polysaccharides. Horner et al. (1975) believed the ligule to be a physiologically active organ which was involved in the movement of selective substances. Goswami (1976) considered the basal portion of the ligule (i.e., the glossopodium) to be a haustorial structure; Sporne (1976) stated that no one knows its true function. Recently Kristen and Biedermann (1981) and Kristen et al. (1982) studied the ultrastructure of the ligule of *I. lacustris* and considered it to be a vestigial organ, which, in extinct genera, might have functioned as a digestive organ.

The ligule is a comparatively well developed structure in *Isoëtes* which occurs above the sporangium on the adaxial surface of the leaf. It has a large, embedded portion called the glossopodium (Bierhorst, 1971; Goswami, 1976). The cells of the glossopodium are isodiametric and distinct from the surrounding cells of the leaf and the labium or velum. Sometimes the glossopodium is surrounded by transfusion cells (Sharma et al., 1980). The free portion of the ligule is a thin, flat, triangular, upward-facing structure parallel to the adaxial surface of the leaf.

MATERIALS AND METHODS

Three species of *Isoëtes,* large *I. coromandelina* L. (JAC 2025), medium-sized *I. rajasthanensis* Gena & Bhardwaja (JAC 2044), and small *I. reticulata* Gena & Bhardwaja (JAC 2052) were studied (Gena & Bhardwaja, in press). The type specimens of the latter species are deposited at Government College, Ajmer, India. *Isoëtes coromandelina* was collected from Daosa, Jhalawar, and Atru, while *I. rajasthanensis* came from Mt. Abu and *I. reticulata* from Atru in Rajasthan. The material was fixed in FAA, and after passing through dehydration alcohol series was embedded in wax. Microtome sections were cut at 8–12 μm (Johanson, 1940) and stained with safranin and Fast green or safranin and haematoxylin. The latter combination was better for studying the ligule.

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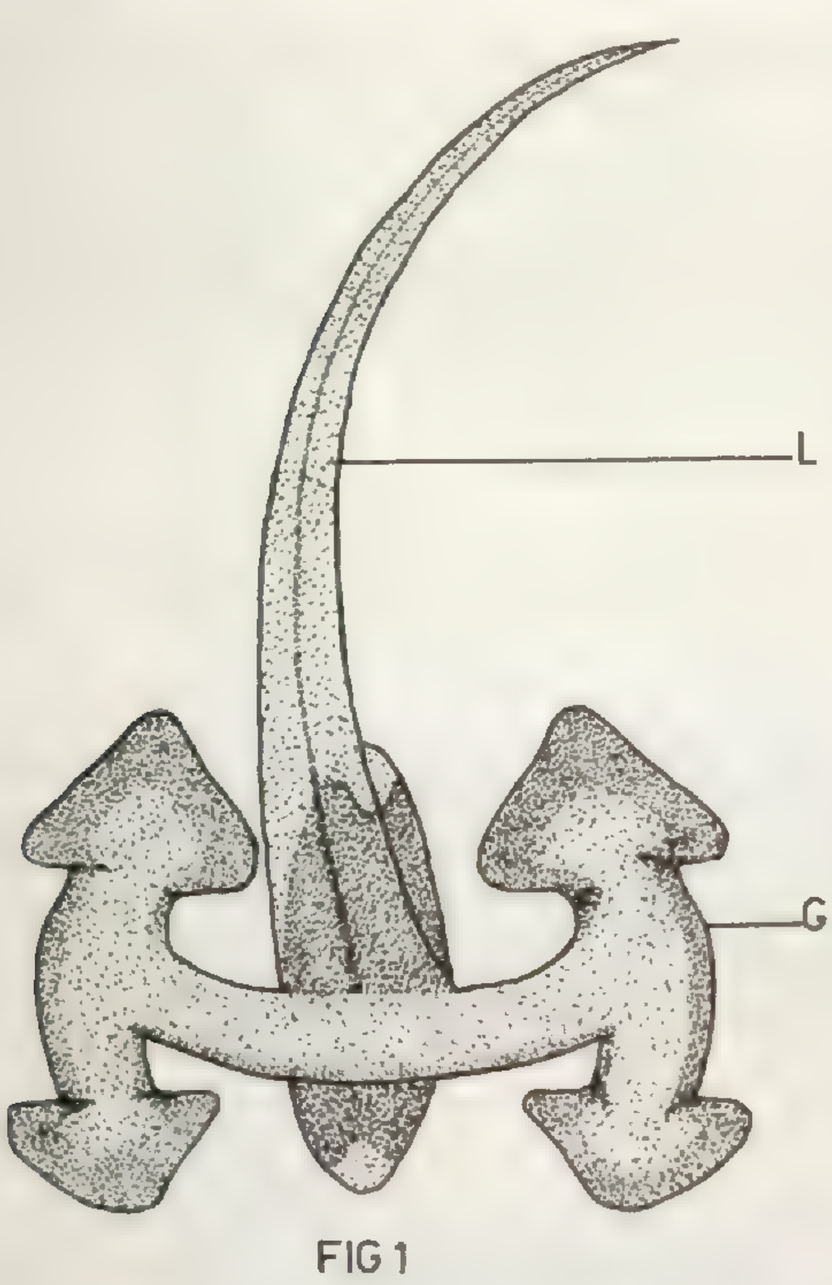


FIG 1

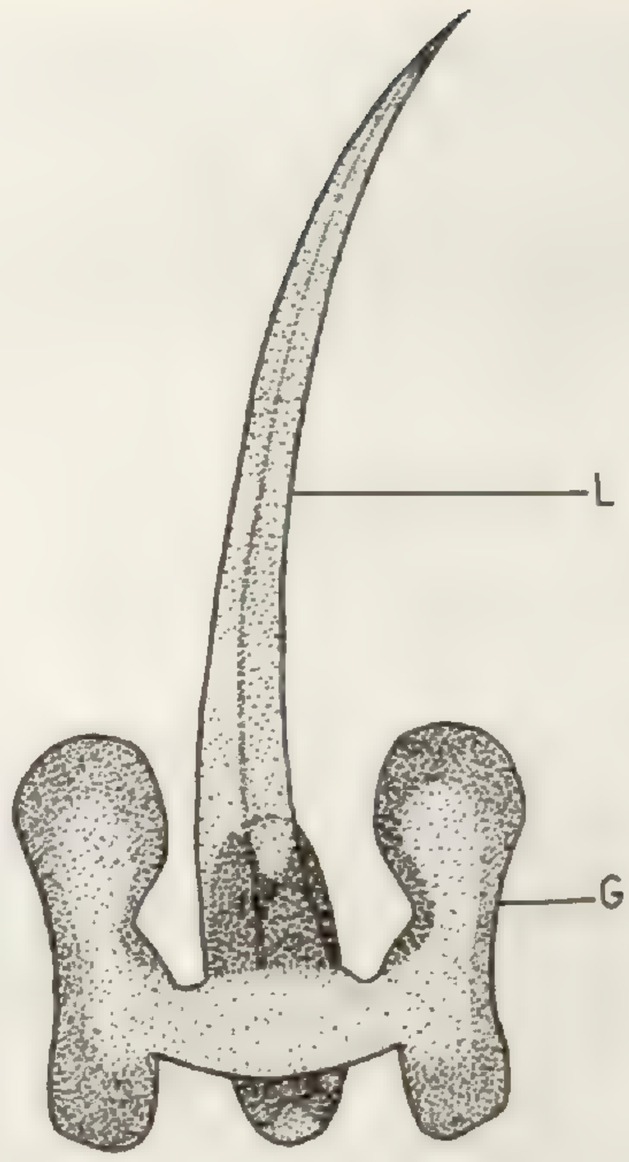


FIG 2

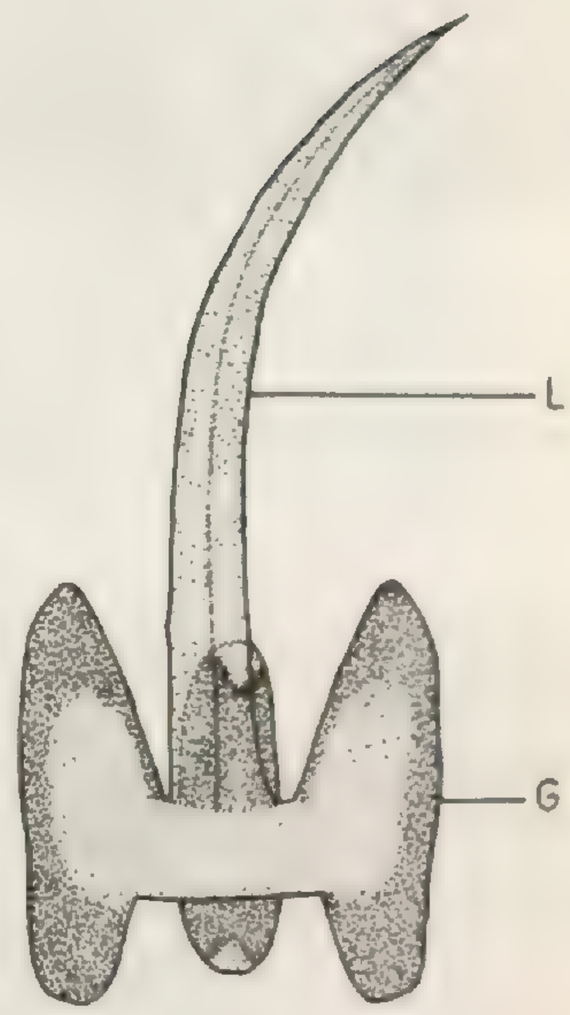


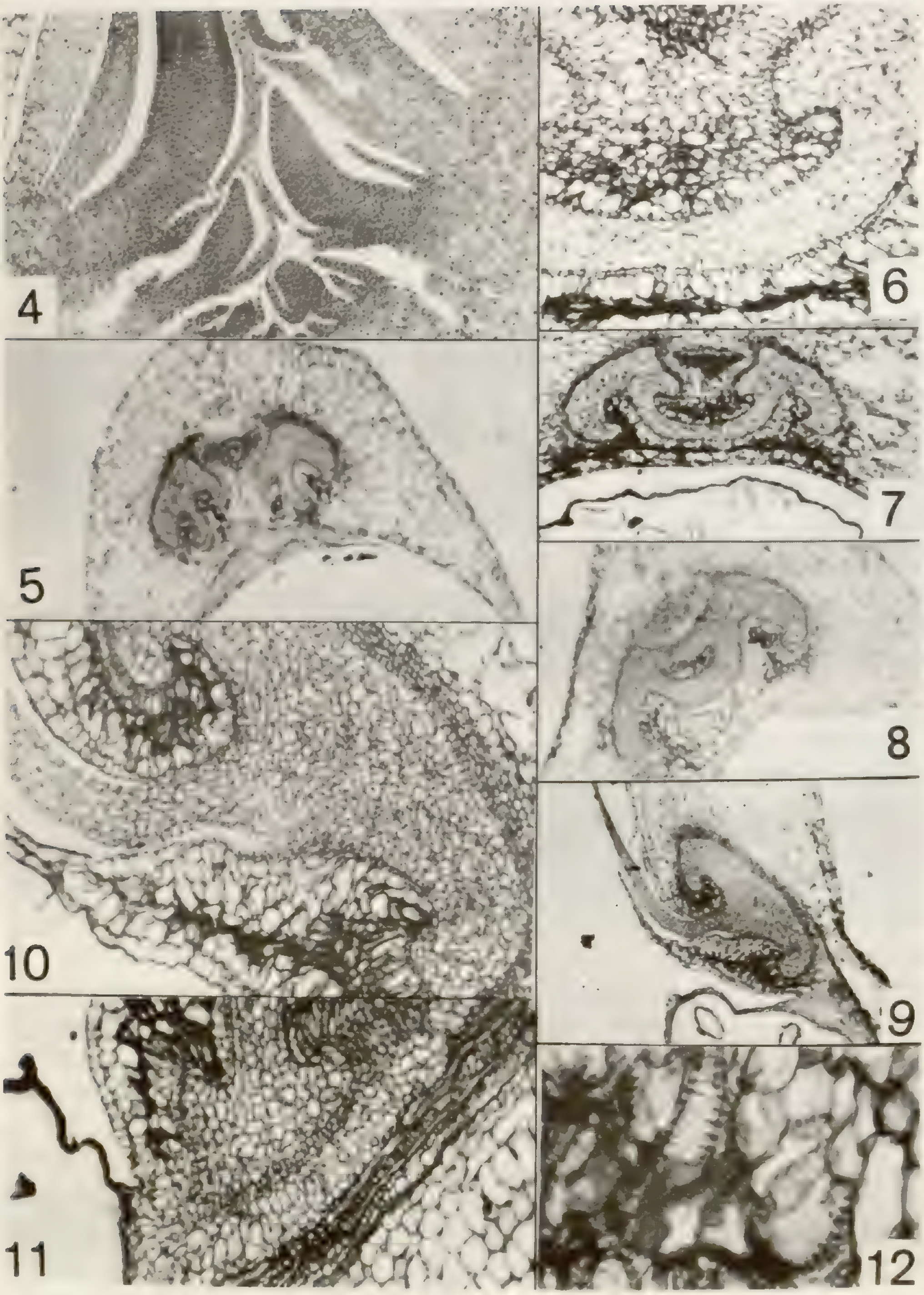
FIG 3

FIGS. 1–3. Reconstructions of *Isoëtes* ligules, ×55. FIG. 1. *I. coromandelina*. FIG. 2. *I. rajasthanensis*. FIG. 3. *I. reticulata*. The abbreviations are: G = glossopodium, L = ligule.

DESCRIPTION

To study the ontogeny of the ligule, serial longitudinal and transverse microtome sections were cut through the rhizomorphs of the three species of *Isoëtes*. In all three species the ligule is fundamentally similar. In none of the species is there a single apical cell, nor is there any plate of apical cells produced (Bhambie, 1957; Paolillo, 1963). The superficial cells divide anticlinally, while the inner cells divide at random. Leaf primordia appear on either side of the apex. The ligule develops from a single initial cell and is differentiated adaxial to the leaf primordium. It divides periclinally, and so a short filamentous structure is produced. In comparison to the leaf, the ligule develops faster; a very young leaf contains an almost fully developed ligule *(Fig. 4)*. In *I. coromandelina* the glossopodium starts to form as two anchor-shaped patches of parenchyma, one on either side of the leaf bundle *(Fig. 5)*. These are then connected by a transverse bar that is 5–7 cells thick *(Fig. 6)*. The anchor-shaped patches also develop a proboscis-shaped structure from the lower side of the bar *(Figs. 7* and *8)*. The bar increases in thickness and forms a large, pad-like structure towards the interior side *(Fig. 9)*, while on the outer side a large flap or whip-like portion of the ligule is produced. The pad remains embedded in the tissue of the leaf. The glossopodium in *I. coromandelina* thus becomes a complicated structure with anchor shaped, curved side arms and a central pad-like portion.

The free, flap-like portion of the ligule and the glossopodium are made up of similar, small, isodiametric, thin-walled cells *(Fig. 10)*. However, the outer 3 or 4 peripheral layers of cells of the glossopodium differ in being comparatively smaller



FIGS. 4–12. Anatomical details of *I. coromandelina*. FIG. 4. Longisection of apical portion of a rhizomorph with young leaves and ligules, ×47. FIG. 5. Cross-section of a leaf showing origin of the glossopodium as anchor-shaped patches of parenchyma, ×13.5. FIG. 6. Cross-section of a leaf showing anchor-shaped patches connected by a bar, ×76.5. FIG. 7. Cross-section of a sporophyll showing glossopodium shape, ×13.5. FIG. 8. Cross-section of a sporophyll showing glossopodium shape, ×13.5. FIG. 9. Longisection of a sporophyll showing the ligule with pad-shaped glossopodium; upper labium is also seen, ×13.5. FIG. 10. Same, showing ligule cells different from those of the labium, which have transfusion cells, ×76.5. FIG. 11. Same, showing the non-vascularized ligule, ×76.5. FIG. 12. Basal portion of a labium with transfusion cells, ×383.

(Fig. 10). The glossopodium does not receive any vascular supply *(Fig. 11)*. However, in *I. coromandelina* it is surrounded by transfusion cells *(Fig. 12)* (Sharma et al., 1980). In this species, the free portion of the ligule is 4.5–6 mm long. Its epidermis is non-stomatiferous, but possesses unicellular and multicellular glandular hairs *(Fig. 13)*.

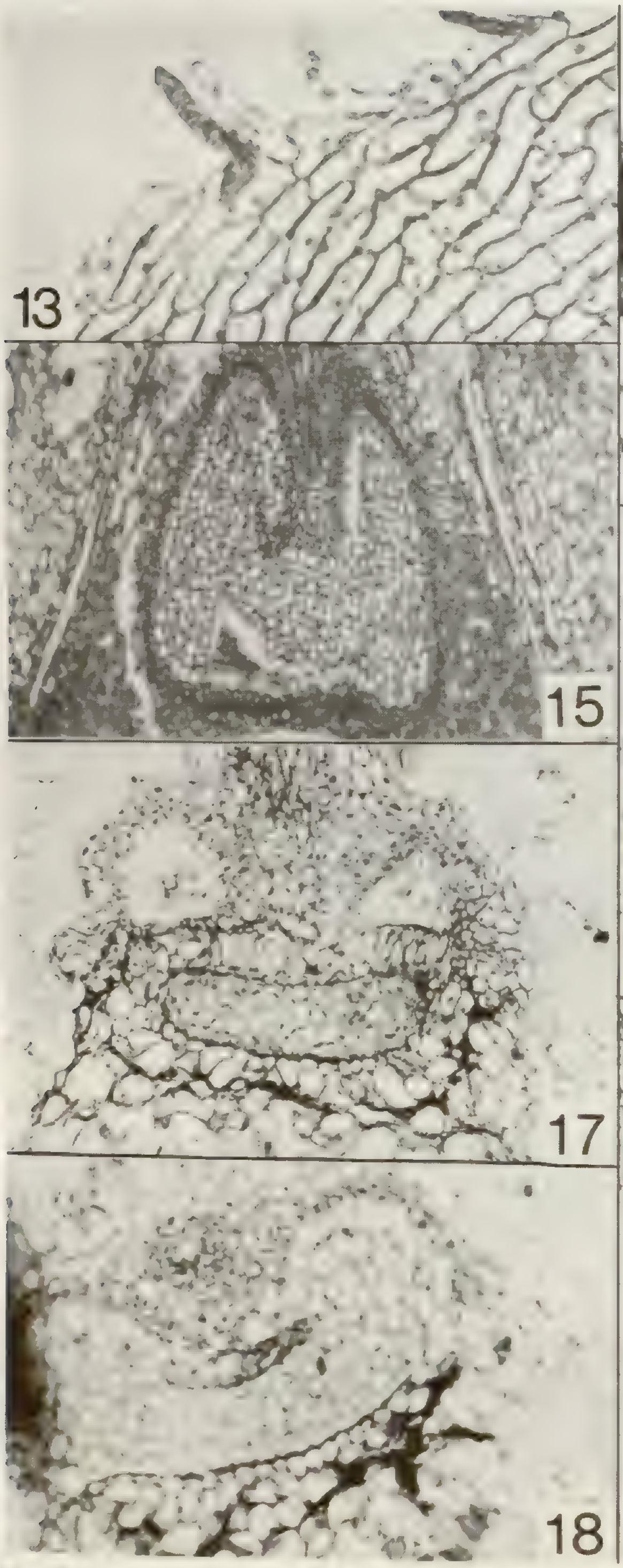
In *I. coromandelina* an upper labium covers the proximal portion of the ligule. In the medium and small-sized species of *Isoëtes,* a distinct velum is present which protects the sporangium *(Fig. 14)*. In the latter species, the ligule is comparatively smaller and the basal portion is less complicated *(Figs. 14* and *15)*. The glossopodium starts to differentiate either as a triangular structure, as in *I. reticulata*, one on either side of the leaf bundle *(Fig. 15)* or as two circular patches of parenchyma, as in *I. rajasthenensis (Fig. 16)*. These structures are then connected by a transverse bar *(Figs. 17* and *18);* as in *I. coromandelina*, an interior, pad-like structure is produced *(Fig. 19)*. However, the glossopodium is not surrounded by transfusion cells.

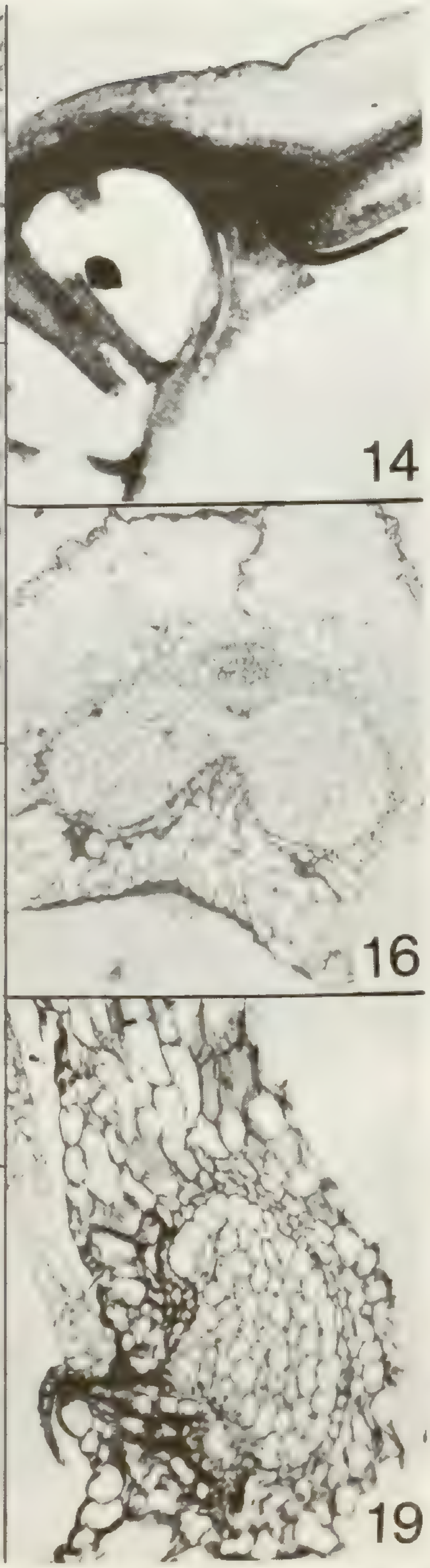
On the basis of the present study, an attempt has been made to reconstruct the structure of the ligule in the three species of *Isoëtes* studied *(Figs. 1–3)*. In *I. coromandelina* the glossopodium is a complex, branched structure and the ligule is quite large. With reduction in plant size, the complexity of the glossopodium and the size of the ligule decrease and the transfusion cells found in association with the glossopodium disappear.

DISCUSSION

Heterospory in pteridophytes originated in the lycopods sometime during the Devonian Period (Pettitt, 1970). The ligule also appeared during the same geological time (Grierson & Bonamo, 1979) and is known to occur in the extinct as well as extant heterosporous lycopods. Whether its occurrence was just a coincidence or whether some relationship really exists between the ligule and heterospory needs further investigation. Recent discovery of a ligule in the presumably homosporous species *Leclercquia complexa* Banks (Grierson & Bonamo, 1972) increases further the importance of this relationship. The structure of the ligule is not well preserved in *L. complexa*, nor can its position on the leaf be related to any of the known ligulate fossil or living genera. Could it be a reduced, sterile telome associated with the fertile telome (sporangium)? In *Lepidostrobus* a number of megaspores were produced per sporangium and the ligule was a small structure, whereas *Miadesmia* had a single megaspore in the sporangium but the ligule was quite elaborated (Scott, 1923; Eames, 1936; Bierhorst, 1971). In *Isoëtes* a large number of megaspores are produced per sporangium and the ligule is also a well developed structure. Thus hardly any parallel can be derived between the evolution of heterospory and the elaboration of the ligule.

In addition to its peculiar type of tracheary elements (Singh et al., 1982), *Isoëtes* is unique in having a velum on the sporangium. In large plants the velum is absent, but the upper labium is present (e.g., *I. coromandelina*, *I. indica*, and *I. pantii*), whereas in comparatively smaller species (e.g., *I. rajasthanensis* and *I. reticulata*) a





FIGS. 13–19. Anatomical details of *Isoëtes* species. FIG. 13. Epidermis of *I. coromandelina* ligule with marginal glandular haris, ×180. FIG. 14. Longisection of an *I. reticulata* sporophyll showing ligule and velum, ×27. FIG. 15. Same, showing glossopodium, ×54. FIGS. 16–18. Cross-sections of *I. rajasthanensis* sporophylls showing different stages of glossopodium development, ×54. FIG. 19. Longisection of an *I. rajasthanensis* sporophyll showing pad-like glossopodium and free portion of ligule, ×54.

distinct velum is present. The elaborated size of the ligule and the complexity of the glossopodium of the larger species may be related to the presence of an upper labium, while reduction in size of the ligule and simplification of the glossopodium in smaller species are probably associated with the presence of a velum. However, this conclusion needs further investigation.

The presence of glandular hairs on both the margins of the ligule favors its secretory function, whereas the occurrence of transfusion cells surrounding the glossopodium (Sharma et al., 1980) and mucilage with polysaccharides (Michaux, 1973) suggest its purpose is a water reservoir to protect the young leaves and sporangia from desiccation. The present study does not favor the haustorial function of the glossopodium, as suggested by Goswami (1976): because the glossopodium cells are small, isodiametric, and uniform, and especially the 2 or 3 layers of cells which occur in the interior portion of the glossopodium are smaller than the surrounding leaf cells. Haustorium cells are generally large and irregular in shape (Maheshwari, 1950).

The absence of a vascular supply and a cuticle in the ligule suggests that it can neither be related to leaf nor to stem. Harvey-Gibson (1896) considered the ligule as a specialized ramentum commonly found in pteridophytes. If this is true then the phylogeny of such a specialized ramentum is yet to be discovered.

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REVIEW

PTERIDOPHYTIC FLORA OF GARHWAL HIMALAYA, by S. S. Bir et al. Jugal Kishore & Co., viii + 83 pp. illustr. 1982. Rs. 95.—This is an account of the pteridophytes in the Garhwal district of Uttar Pradesh, India (78–79° E Long, 30–31° N Lat), especially of the area within 50 km of the town of Mussoorie, an old and ever popular collecting locality. The region mostly lies at 600–2400 m elevation and has a tropical or subtropical monsoon climate. A total of 157 pteridophytes, many of them widespread species, are enumerated, and others whose presence in the region is problematical are mentioned. No new taxa are described. The generic name *Microsorum* Link (1833), rather than *Microsorium*, is adopted following Sledge (1960) and Pichi Sermolli (1977), although Link (1841) did correct the original spelling to *Microsorium*. A map of the region, photographs of some of the species, and an index conclude the volume, which is available from Jugal Kishore & Co., 23-C Rajpur Road, Dehra Dun, India.—*D.B.L.*

SHORTER NOTES

TWO SPECIES OF ADIANTUM NEWLY ESCAPED IN FLORIDA.—Two previously unrecorded species of *Adiantum* have recently been discovered near Homestead in southern Dade County, Florida. Both are commonly cultivated tropical species known from single sites, so the plants almost certainly are escapes from cultivation.

Adiantum trapeziforme L. was discovered by the late George N. Avery in February 1980. He found a single plant growing at the top of a low spoil bank in an area kept humid by runoff from a nearby water-pumping station, and he collected a single fertile frond (*Avery 2207*, FTG). The fern grows in an area shaded by the exotic weed trees *Schinus terebenthifolius* and *Albizzia lebbeck*. Avery took us to see the plant in late 1982; we visited the site again in January 1984. Both times we looked for evidence of young *Adiantum* plants. No sporelings were ever found, although the original plant appears to be growing well and produces spores regularly. The *Adiantum* might represent a persistent plant from cuttings dumped at the site, but, as no evidence for dumping was found, we concluded that the plant is a true escape. The future of this species in South Florida is problematical. It grows in a relatively protected area and is not likely to be destroyed by human activities in the near future, but it apparently has not spread in the four years since its discovery. Whether it is capable of becoming truly naturalized is not clear.

In March 1983 the senior author found approximately seven plants of *Adiantum anceps* Maxon & Morton growing on the vertical walls of trenches cut into rocky ground, along with *Ctenitis sloanei* (Poeppig ex Sprengel) Morton. The plants were growing in the shade of *Schinus terebenthifolius*. Undoubtedly water collecting at the bottom of the trenches helped maintain a humid environment. Two voucher specimens have been collected (*Herndon 702* and *Avery 2501*, FTG). This species has spread within its rather specialized habitat, suggesting that the climate in South Florida is conducive to its growth. The colony is in an area of active commercial development and will likely be destroyed before the plants spread to more protected areas. Still, the habitat in which the plants grow is quite similar to the "pinnacle rock" areas found in some Dade County parks. Given the continuous supply of spores from cultivated plants and the availability of apparently suitable habitat in protected areas, it is likely that this species will sooner or later become an established member of our naturalized flora.—*Alan and Rhonda Herndon, 15301 S.W. 306th St., Homestead, FL 33033.*

A NEW STATION FOR TRICHOMANES PETERSII IN ALABAMA.—The filmy fern *Trichomanes petersii* A. Gray (Hymenophyllaceae) was first described from Winston County, northern Alabama, and the fern occurs most abundantly in the northern part of that state. Nevertheless, relatively few stations are known, and the plant is considered rare and endangered by Dean (Ferns of Alabama and Fern Allies, 1964, p. 31) and by Short (Distribution of Alabama Pteridophytes, M.S. Thesis, Auburn University, 1978, p. 105). The entire range of *T. petersii* in the United States includes North and South Carolina, Georgia, Florida, Tennessee, Illinois, Arkansas, Mississippi, and Louisiana. Only a single station is known in many states.

While doing fieldwork in the vicinity of Tuscaloosa on 12 November 1983, I discovered a dense colony of *T. petersii* covering a standstone boulder in a small, north-facing ravine ca. 0.1 km south of Holt Lock and Dam on the Black Warrior River at an elevation of ca. 65 m, in Tuscaloosa Co., west-central Alabama (*Wyatt 1622*, AUA, GA, NCU, UNA).

The new collection extends the range of *T. petersii* approximately 100 km south of the areas of its greatest abundance on the Sipsey Fork of the Black Warrior River. Its occurrence in the Fall Line Hills of Tuscaloosa County on the southern edge of the Cumberland Plateau parallels its restriction to ravines near the western (Franklin, Lawrence, Winston, and Lamar Cos.) and eastern (DeKalb and Etowah Cos.) edges of the Plateau. The only exception in Alabama is the collection by Correll (Amer. Fern. J. 29:141. 1939) from the Valley and Ridge Province in Cleburne County. All collections appear to be from sandstone of the Pennsylvanian Upper Pottsville Formation.

The steep, protected ravines of the Holt Lake area north of Tuscaloosa harbor a number of rare or disjunct angiosperms, including *Neviusia alabamensis* A. Gray, *Croton alabamensis* E. A. Smith ex Chapman, *Cladrastis kentuckea* (Dum.-Cours.) Rudd, and *Aesculus parviflora* Walter (Brooks, A Checklist of the Vascular Plants of the Holt Lock and Dam Area, Tuscaloosa County, Alabama. M. S. Thesis, Univ. of Alabama, 1969, p. 46). Fortunately, construction of the Holt Dam did not flood the ravine in which *T. petersii* occurs, as happened at the type locality for this fern (Dean, Ferns of Alabama and Fern Allies, 1964, p. 31) and for *Leptogramma pilosa* var. *alabamensis* (Crawford) Wherry (Short & Freeman, Amer. Fern J. 68:1–2. 1978) on Sipsey Fork in Winston County. It is possible that *T. petersii* occurs at additional sites on the Black Warrior River north of Holt Lock and Dam and that this very diminutive fern has simply been overlooked. In addition to the seven counties for which herbarium records are known, attempts should be made to document literature reports for Marion Co. by Mohr (Contr. U. S. Natl. Herb. 6:319. 1901), Marshall Co. by Graves (Amer. Fern J. 10:78. 1920), and Walker Co. by Dean (Ferns of Alabama and Fern Allies, 1964, p. 174).

I thank Ann Stoneburner and Ireneusz J. Odrzykoski for field assistance and Robert R. Haynes for advice. A grant from the Whitehall Foundation helped make this research possible.—*Robert Wyatt, Department of Botany, University of Georgia, Athens, GA 30602.*

TRICHOMANES GAMETOPHYTES AT BARTHOLOMEW'S COBBLE.—Distribution of the little known asporophytic fern gametophytes of *Vittaria* and *Trichomanes* in the northeastern United States was recently described by Farrar, Parks, and McAlpin (Rhodora 85:83–91. 1983). Their study was prompted by the discovery in 1976 by McAlpin and Farrar of *Trichomanes* gametophytes in Franklin County, Massachusetts, more than 400 miles above the previously known northernmost station (Amer. Fern J. 68:4. 1978). Both *Trichomanes* and *Vittaria* reproduce asexually by gemmae, which develop on the gametophyte, and are not known to develop sporophytes throughout their northeastern distribution. They are typically found on heavily shaded, moist outcroppings of non-calcareous rock, often deep in crevices or small caves. During the summer of 1982, I discovered a second Massachusetts station for *Trichomanes* at Bartholomew's Cobble in southern Berkshire County on rocks which are recognized as largely calcareous. This discovery is of interest because of the historic nature of the site and because of the apparent problem of the gametophytes growing on the "wrong substrate."

Bartholomew's Cobble was aptly described by Weatherby (Amer. Fern J. 37:1. 1947) as a picturesque natural preserve located in the southwestern corner of Massachusetts in the Housatonic River valley, several miles from Ashley Falls. Like other cobbles in the valley, it is formed as a rocky hill projecting from the underlying limestone. It is a National Natural Landmark protected and administered by The Trustees of Reservations of Massachusetts and is recognized by field naturalists for its impressive natural concentration of plants. Weatherby (Amer. Fern J. 37:1. 1947) cited a total of 276 species of flowering plants and ferns within the 25 acre preserve; however, literature distributed at the Cobble boasts almost 500 wildflowers, 100 kinds of trees, and 49 species of ferns and fern-allies, including somewhat elusive specimens of Scott's Spleenwort.

During the summer of 1982, while hiking the picturesque Ledges Trail overlooking the Housatonic River, I was attracted to investigate the little pockets and caves scattered around the outcrops, which are covered with various ferns and other plants. Having recently accompanied Dr. Donald Farrar in the field in Lancaster County, Pennsylvania, where he was studying the distribution of *Trichomanes* and *Vittaria*, I developed some skill in their field identification. To my surprise, I discovered the typical little fuzzy green tufts of *Trichomanes* growing on the sidewalls of several of these little "limestone" caves. These tiny plants are superficially very moss-like and may be easily overlooked; however, with a good hand lens and a little experience, they can be readily recognized. Farrar (pers. comm.) has indicated that neither *Trichomanes* nor *Vittaria* have ever been reported on a calcareous substrate.

I was pleasantly surprised to discover that Wherry reported a somewhat similar incongruity when he discovered acidophilic Spike-moss *(Selaginella rupestris)* growing on the same ledges of Bartholomew's Cobble (Amer. Fern J. 41:1. 1951). The explanation, he found, was that acid soils accumulate in the pockets formed in the veins of milky-white quartz mingled with the limestone. It was in these very pockets that I discovered the *Trichomanes*. Dr. Wherry warned against erroneous inferences as to the soil preference of individual species on the basis of superficial

observations. I would like to think he would be pleased that another acid-loving plant was discovered growing on this predominantly limestone cobble.

Bartholomew's Cobble is surely an atypical site for *Trichomanes*. And yet, as field naturalists become more familiar with these interesting little ferns and involved in the search for new sites in the interest of extending the distributions recently mapped by Farrar, et al. (Rhodora 85:83–91. 1983), we do well to note Wherry's warning and not overlook habitats on the assumption that they are calcareous and therefore unfavorable to *Trichomanes*.—*Kenneth G. Miller, Roddy Science Center, Millersville University, Millersville, PA 17551.*

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A Western Holly Fern, Polystichum ×scopulinum, in Newfoundland

WARREN H. WAGNER, JR.* and ERNEST ROULEAU**

The holly ferns of North America have recently received considerable study (W. Wagner, 1973; D. Wagner, 1979), which has resulted in a number of changes in their taxonomic interpretation. In the west, 11 sexual taxa are recognized, in the east only four. Three of the latter are northern, occurring mainly in Canada. The fourth, the familiar Christmas Fern, *P. acrostichoides* (L.) Schott, with distinctive semi-dimorphic leaves, is southern in distribution and is by far the most abundant and widespread member of the genus. The rarest Holly Fern in the east is the mainly western Hybrid Holly Fern *P.* ×*scopulinum* D. C. Eaton (fertile tetraploid form), known previously from a single mountain on the Gaspé Peninsula of Quebec. This disjunct has attracted much attention because it is separated by over 2000 miles (3200 km) from its range in the western United States and southwestern Canada. Fernald (1924) considered it a relict which had survived the Ice Age on an unglaciated mountain or "nunatak."

Fernald (1924, p. 89) considered *P.* ×*scopulinum* a northern variety of the southern hemisphere *P. mohrioides* (Bory) Presl, stating that "this anomalous plant [var. *scopulinum* (D. C. Eaton) Fern.] . . . has been treated as a variety of *Polystichum aculeatum* or of *P. lonchitis*, as *P. mohrioides* and as a distinct species standing midway between *P. aculeatum* and *P. mohrioides*." W. Wagner (1973) found that *P. scopulinum* is actually a hybrid, with one parent *P. mohrioides s. l.* and the other *P. munitum* (Kaulf.) Presl *s. l.*[1] The hybrid origin of *P.* ×*scopulinum* was deduced from a number of data which show that it is an allopolyploid intermediate between the parents. In expeditions with A. R. Kruckeberg in serpentine areas of Washington state backcrosses of *P.* ×*scopulinum* with its parents and also primary sterile diploid hybrids were found. Thus, *P.* ×*scopulinum* occurs both in a sterile diploid form and a fertile tetraploid form, the latter having the ability to disperse and reproduce sexually.

The occurrence of *P.* ×*scopulinum* is of special interest because the polyploid hybrid occurs so far from its parents. Similarly, Wright's Cliff-brake, *Pellaea ternifolia* (Cav.) Link, is known from two stations in North Carolina some 1000 miles (1600 km) east of its metropolis in the southwestern United States (Wagner, 1965, 1972).

Polystichum ×*scopulinum* occurs on Mt. Albert in the Shickshock Mountains of the Gaspé Peninsula, where it has been collected many times. The colonies grow on serpentine cliffs and rock slides in ravines at altitudes of 2000–3000 ft. At a

[1]David Wagner (1979) interpreted the North American *P. mohrioides* as distinct from that in South America and treated it as *P. lemmonii* Underw. The variety of *P. munitum* known traditionally as var. *imbricans* D. C. Eaton he considered to be a distinct species, *P. imbricans* (D. C. Eaton) D. Wagner. He thus give the hybrid formula as *P. imbricans* ×*lemmonii*.

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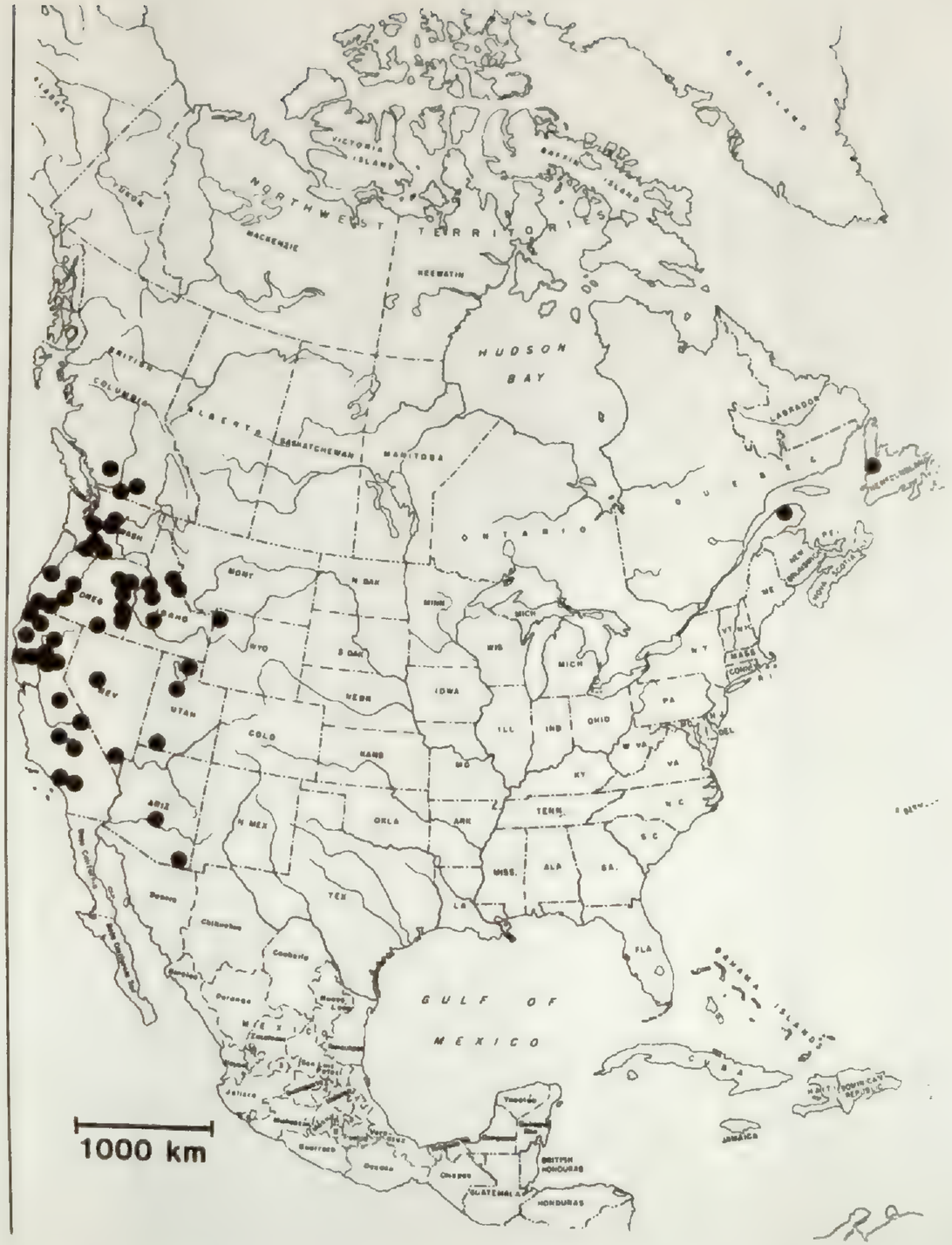

FIG. 1. *Polystichum* ×*scopulinum*, southerly slopes of dry serpentine ridge, near the head of North Arm, Newfoundland, *Rouleau 884* (MT). FIG. 2. Known range of *Polystichum* ×*scopulinum*, including new record from Newfoundland.

distance, the plant may be confused with *P. lonchitis* (L.) Roth, a common northern species, and thus may be overlooked in routine collecting. It may also superficially resemble exposed or dwarfed forms of *P. braunii* (Spenner) Fée, a fern with bipinnate, thinner-textured, and scalier fronds. These three species are contrasted in Fernald's key (1950, p. 37).

Rouleau found *P. ×scopulinum* for the first time in Newfoundland on 18 July 1950 while exploring the southerly slopes of a dry serpentine ridge near the head of North Arm in the Humber District (*Rouleau 884*, MT). The plant resembled a small, fertile *P. braunii* (*Fig. 1*), and its true identity was not recognized until March 1978. Rouleau has found both *P. braunii* and *P. lonchitis* to be common and widespread in Newfoundland, but thus far he has collected *P. ×scopulinum* only at this single site. This discovery extends the known range of *P. ×scopulinum* nearly 400 miles (560 km) northeast of the colony on Mt. Albert in Quebec. Although fully fertile, the herbarium specimen is smaller than average for this species. The stipes are unusually long, nearly equal in length to the blades, presumably as a result of growing in a deep pocket. The pinnae of the lower half of the blade are strongly auricled at the anterior base, and some of the auricles are contracted basally to a stalk.

A distribution map (*Fig. 2*) of *P. ×scopulinum* based on records from W. Wagner (1973), D. Wagner (1979), Taylor (1970), and the Newfoundland specimen shows not only the vast disjunction between west and east and the far greater number of localities in the west, but also the extension of the taxon in the west to much lower latitudes.

Damman (1965), in his review of distribution patterns in the flora of Newfoundland, recognized a category of species that are restricted to serpentine areas, to which *P. ×scopulinum* must now be added. He described the habitats as bleak and exposed with sparse vegetation. He believed that serpentine species occur on these sites because of a "lack of competition, the basic soils, and their ability to tolerate frost churning." Damman discussed Fernald's "Nunatak Theory" and concluded from reports by a number of workers that Fernald's nunatak areas had been covered with ice at some time or other during the glacial period.

Rather than assume that *P. ×scopulinum* persists as a relict on a Newfoundland nunatak, it may be more reasonable to attribute the occurrence of *P. ×scopulinum* to long distance dispersal by spores. Bouchard et al. (1977) recently gave another striking example of probable long distance dispersal in Newfoundland: *Thelypteris limbosperma* (Allioni) H. P. Fuchs [syn. *Oreopteris limbosperma* (Allioni) Holub] was unknown in eastern North America until 1973, when a large colony was found in Gros Morne National Park. The species is known to occur otherwise in North America only from Alaska to central Washington.

In view of the number of examples now known of west to east disjunctions in Canada and the United States and the evidence that single spores have the potentiality for establishing new colonies (Wagner, 1972), the presence of *P. ×scopulinum* in the east seems no longer as exceptional as it was once thought to be. The existence of this fern in Newfoundland several hundred miles from its nearest other colony could have resulted from a wind-blown spore from as close as the Gaspé Peninsula or as far as the west coast of North America.

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REVIEW

FERNS AND FERN ALLIES OF GUATEMALA, PART III. MARSILEACEAE, SALVINIACEAE, AND THE FERN ALLIES (INCLUDING A COMPREHENSIVE INDEX TO PARTS I, II, AND III), by Robert G. Stolze. Fieldiana: Botany, NS, 12. 91 pp. 1983.—This is the final part of the Ferns and Fern Allies of Guatemala, and includes the heterosporous ferns and fern allies—eight genera in all—plus an index to all parts. *Lycopodium* is treated by B. Øllgaard and *Isoëtes* with the help of R. J. Hickey. The third part follows the first two in format (Part I reviewed in Amer. Fern J. 67:94, Part II in 72:14), and the clear, concise style is maintained here also. I found no errors of consequence. The keys seem well constructed with contrasting statements in each pair of leads. I tried several species of *Lycopodium* and found no problems in use.

A nice feature is the discussion within the generic treatments of excluded species in *Marsilea*, *Azolla*, and *Salvinia* which have not been found but could be expected in Guatemala, and how these could be distinguished from included taxa. Stolze also points out the need for monographic work in these genera and the difficulties in taxonomy and identification when much (most in *Azolla*) material is vegetative only.

The author is to be commended on the completion of this important work on tropical American pteridophytes. Stolze's *Ferns and Fern Allies of Guatemala* and Alan R. Smith's *Flora of Chiapas—Pteridophytes* have made an excellent start on filling in our knowledge of the ferns on this region.—*James D. Montgomery, Ichthyological Associates, Inc., Berwick, PA 18603.*

Drymoglossum Under Water Stress

C. S. HEW*

Drymoglossum is an epiphytic fern found commonly on the trunks of some local trees. It exhibits typical CAM features (Hew & Wong, 1974; Wong & Hew, 1976). It has fleshy fronds for storing water, but it is not uncommon to observe shrivelling of its fronds during dry spells.

Different CAM plants seem to respond to drought differently. Under water stress, CAM plants such as *Tillandsia* increase their CAM activities, but plants such as *Opuntia* reduce their CAM activity instead (Kluge & Ting, 1978). We have reported recently that tropical succulent orchids behave just like *Opuntia* when placed under water stress (Fu & Hew, 1982).

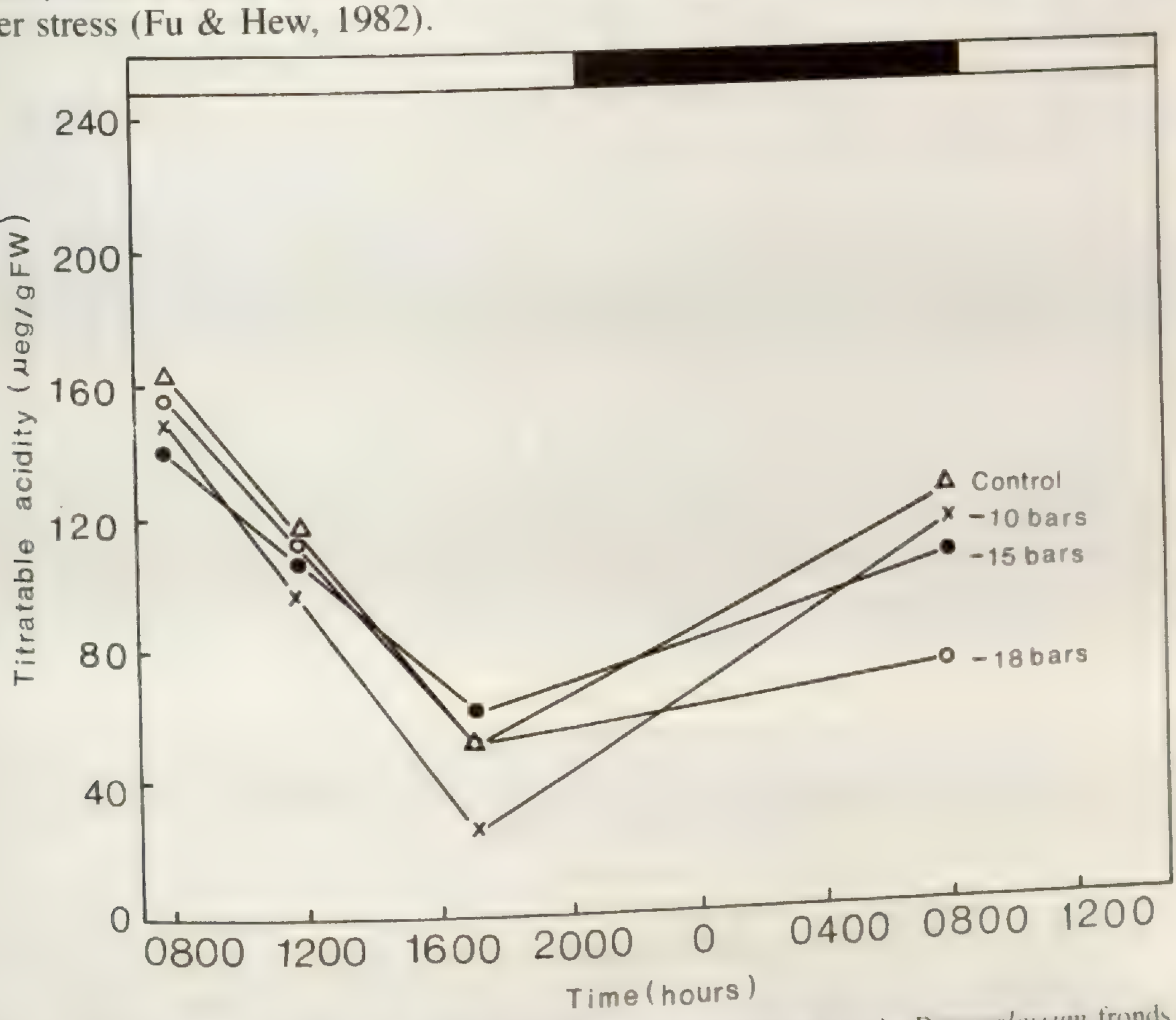

FIG. 1. Effect of water stress on diurnal fluctuation of titratable acidity in *Drymoglossum* fronds after imposing two days of water stress.

Inhibition of protein synthesis and changes in amino acid metabolism are aspects of metabolic changes in plants which have been extensively studied in relation to water stress (Hsiao, 1973). Accumulation of proline concentration was the main reason for the increase of free amino acids (Singh et al., 1973a, b). Proline accumulation is a result of a stimulation of its synthesis and an inhibition of its utilization (Stewart, 1980). Works on proline accumulation under water stress have

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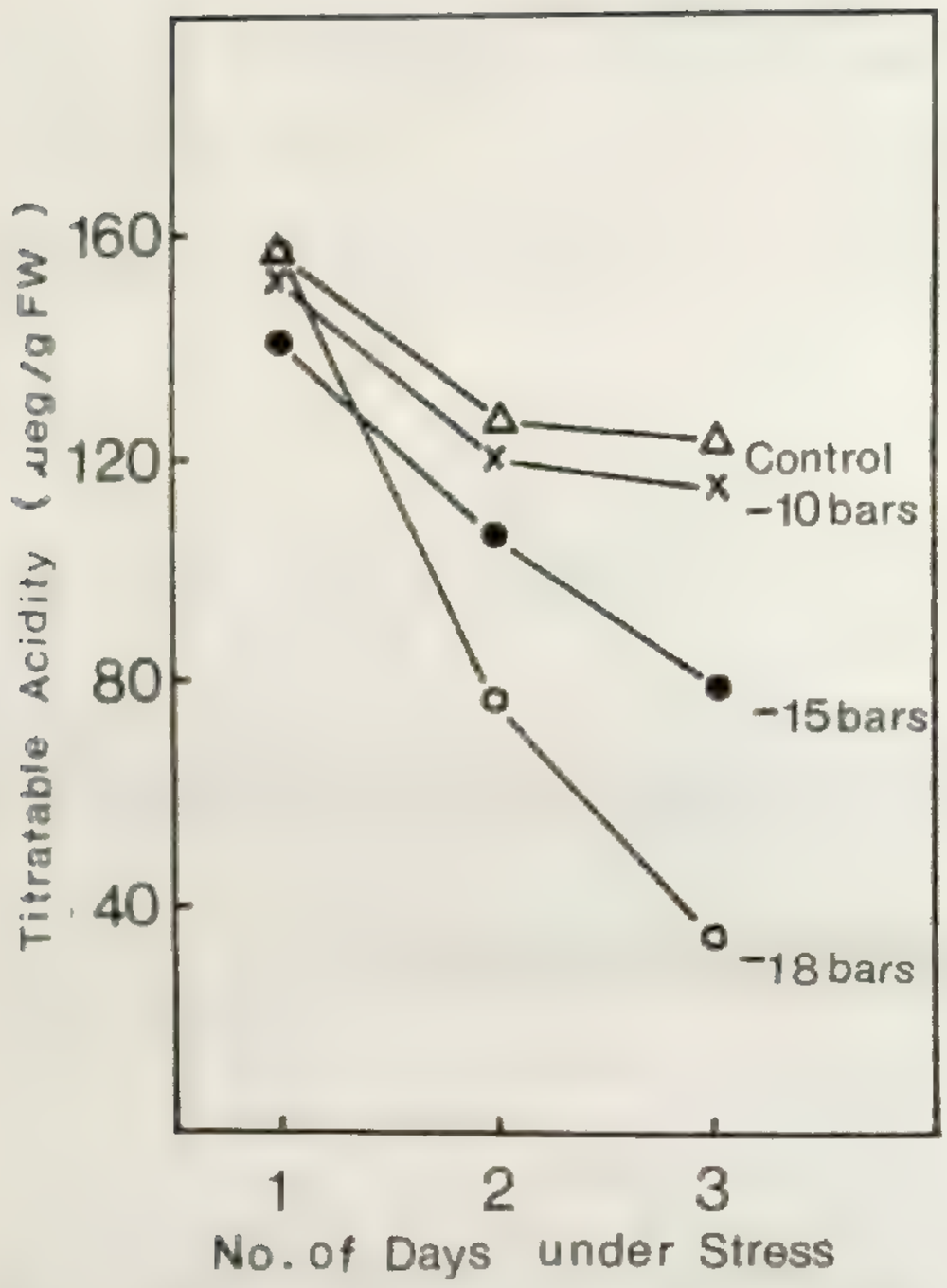

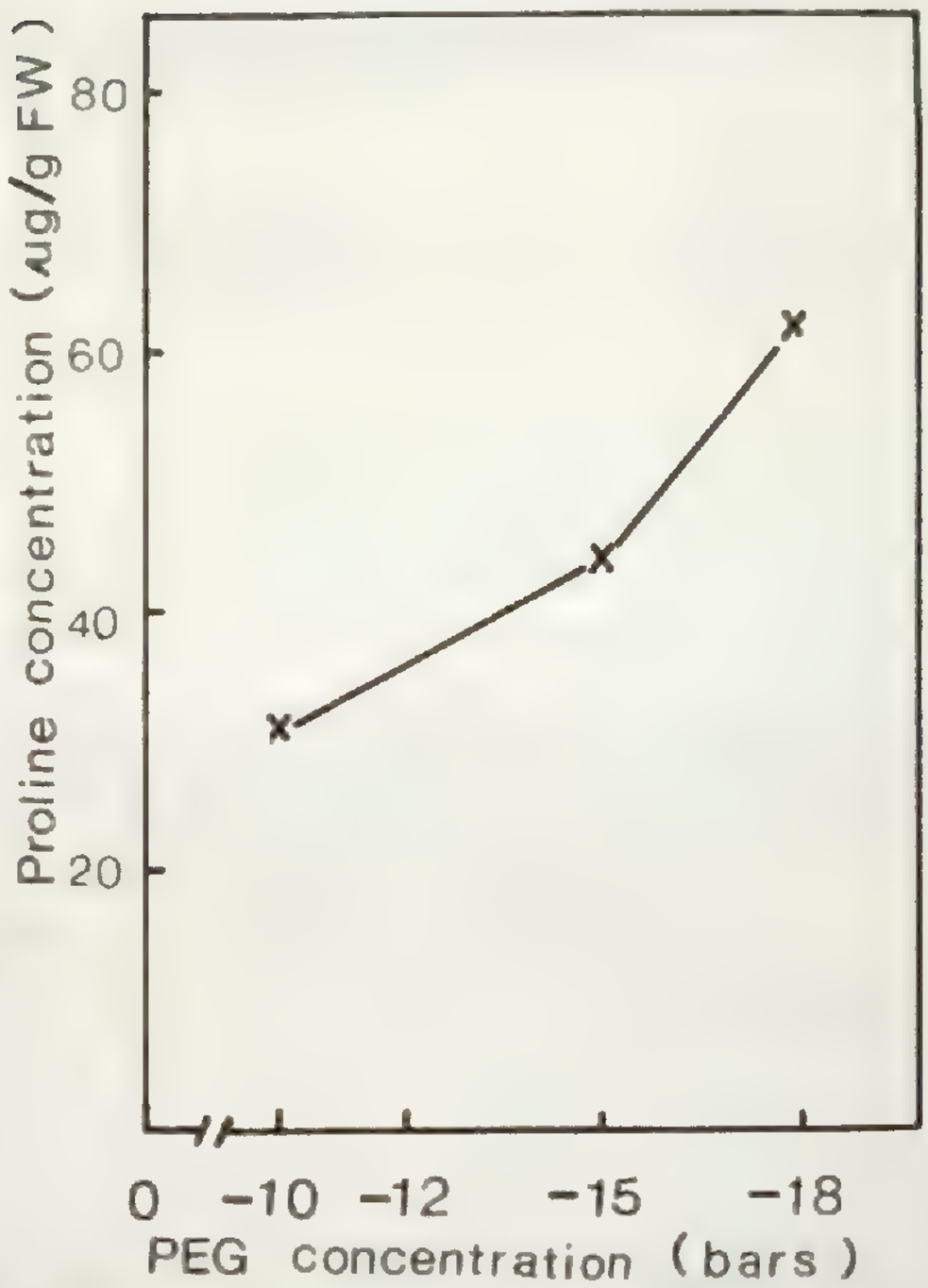

FIG. 2. Effect of length of time of water stress on titratable acidity in *Drymoglossum* fronds. FIG. 3. Proline accumulation in *Drymoglossum* fronds under various PEG concentrations 56 hrs after imposition of water stress.

been carried out with *Chlorella* (Greenway & Setter, 1979), barley (Hanson et al., 1977; Singh et al., 1973a, b; Tully et al., 1979), Bermuda grass (Barnett & Naylor, 1966), halophytes (Cavalieri & Huang, 1979), spinach (Huang & Cavalieri, 1979), and tobacco (Boggess & Stewart, 1980). This paper reports the effect of water stress on CAM activity and proline accumulation in *Drymoglossum*.

Sterile, mature fronds of *Drymoglossum piloselloides* (L.) Presl were collected from *Acacia* tree trunks. Eight uniform-sized fronds were placed in each petri dish with filter paper serving as substratum. These were kept in a temperature-controlled room (26° C) with a 12 hr photoperiod and at a light intensity of 1200 ft-c. The light source was a 700-watt HPLR mercury lamp.

Water stress was imposed by placing the fronds in various concentrations of polyethylene glycol (PEG) 1000, giving a range of osmotic potential from about −10 bars to −18 bars. The control was kept in distilled water. All treatments were done in triplicate.

Titratable acidity was measured as described by Wong and Hew (1976). The extraction and determination of proline were done according to the method described by Singh et al. (1973a) and by Troll and Lindsley (1955). Unless stated otherwise, measurement of titratable acidity was done at 0800 hr.

Both controls and stressed plants displayed pronounced diurnal fluctuation of titratable acidity (*Fig. 1*). Pronounced decrease in titratable acidity was observed 2 days after water stress. Titratable acidity decreased with a corresponding increase in PEG concentration and with days of water stress (*Figs. 1* & *2*). The decrease in titratable acidity in *Drymoglossum* under stress, therefore, resembled that of tropical orchids (Fu & Hew, 1982). The drop in titratable acidity in water-stressed

Drymoglossum could also be attributed to a decrease in CO_2 fixation, as has been observed in orchids (Fu & Hew, 1982) and in other plants (Osmond, 1978).

Proline accumulation increased in fronds of *Drymoglossum* following water stress (*Fig. 3*). This is in agreement with previous reports obtained for barley, grass, wheat, spinach, and tobacco. Our findings support the generalization that most if not all plants have the ability to accumulate proline, provided that the imposed water stress is severe enough (Hsiao, 1973).

Proline accumulation in succulent halophytes under stress has been reported (Cavalieri & Huang, 1979), but it is yet to be shown that the succulent halophytes exhibit CAM features (Webbs & Burley, 1965). We now have evidence to indicate that under PEG stress, CAM plants such as *Drymoglossum* start to accumulate proline around -10 to -15 bars. The same has also been observed for succulent tropical orchids, also CAM plants (Hew, unpublished data).

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Problems in Asplenium, with Some New Species from Ecuador

ROBERT G. STOLZE*

While studying the genus *Asplenium* for the "Flora of Ecuador," I encountered great difficulties with circumscription of *A. myriophyllum* (Swartz) Presl. This is a highly dissected species of wet forests, reported from Florida, the Greater Antilles, Mexico, much of Central America, Colombia, Venezuela, Ecuador, and Peru. It occurs rather frequently throughout much of its range, has several very close relatives, and is itself highly variable. Among its most diagnostic characters are: tripinnate or subtripinnate (often only bipinnate in Florida) laminae rather abruptly reduced at the base; dull grayish or reddish brown petioles up to 15 cm long; castaneous to blackish, rather shiny, scarcely clathrate rhizome scales; and pinnae about 20–25 pairs, mostly ascending, sessile, with the basal pinnules overlapping the rachis.

Asplenium myriophyllum has been found in herbaria, often identified as *A. cladolepton* Fée, *A. cristatum* Lam. (syn. *A. cicutarium* Swartz), *A. divaricatum* Kunze, and *A. rutaceum* (Willd.) Mett. (syn. *A. conquisitum* Underw. & Maxon ex Christ). It is easy to understand the confusion, for these species share many similar features, and whereas each seems to be readily identifiable in the typical habit, there can always be found several collections in which characters tend to merge with those of other species in the group. *Asplenium rutaceum* (common in the neotropics) is the most distinctive, as it is the only species which has highly lustrous, castaneous to blackish petioles and lower rachises. Furthermore the lamina is strongly and gradually reduced to a naked and flagelliform apex, this often with a proliferous tip. In the other species of the group, the petiole is dull and lighter in color, and the lamina tapers to a pinnatifid apex—this sometimes attenuate, but never flagelliform and radicant.

Asplenium cristatum (also with wide distribution in the neotropics) is the next most distinctive of the species listed above, as the lamina is scarcely, if ever, reduced at the base; i.e., the basal pair of pinnae are nearly or quite as long as the central ones. The lamina in all the other species is strongly (either gradually or abruptly) reduced at base, with two to many proximal pairs of pinnae conspicuously shorter than the central ones. Nevertheless, I have found several specimens of *A. cristatum*, from Guatemala to Ecuador, in which one or two proximal pairs of pinnae are significantly reduced.

Asplenium cladolepton and *A. divaricatum* are species which more properly might be considered variants of *A. myriophyllum*. The former, known from Colombia, Venezuela, and rarely in Ecuador, differs from *A. myriophyllum* primarily in its smaller size and narrower lamina. The epipetric Peruvian species, *A. divaricatum*, appears to be a depauperate *A. myriophyllum* with leaves only 3–10 cm long and tiny ultimate segments. It may be merely an ecological variant.

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Asplenium myriophyllum varies strongly throughout its range. Many collections from Florida and Guatemala are much smaller and often only bipinnate, whereas leaves in South American plants are typically luxuriant, up to 40 cm long and fully tripinnate. Petioles are commonly 8–15 cm long, yet those of some plants from Florida and the Greater Antilles measure only 2–3 cm. It is no wonder then that ferns in this group are universally misunderstood. Obviously detailed research is needed, in which comparisons are made of specimens throughout the neotropics. Furthermore, it is probable that much hybridization is occurring here—a situation not uncommon in the genus. Mickel ("How to Know the Ferns and Fern Allies," p. 56. 1979; Wm. C. Brown, Dubuque, Iowa) delineates several known hybrids in North America which involve *A. myriophyllum*. But no such studies have been undertaken yet throughout the broad range of its distribution.

One should be cautious in naming a new species within a group already so confused. However, in studying the genus for "Flora of Ecuador," I came upon a large number of Ecuadorean specimens which appeared to be clearly distinct in lamina architecture from the other components of the species complex. These were variously determined as *A. cicutarium*, *A. conquisitum*, *A. cristatum*, *A. myriophyllum*, *A. rhizophyllum*, and *A. rutaceum*. As herbarium specimens were separated on the basis of obvious morphological features, other, less obvious, characters came to light, which convinced me that this was a species much more distinct than most others already recognized in the group. Oddly enough, although it has been collected frequently in Ecuador, I can find no record of its occurring in neighboring countries.

Figs. 1–3.

Asplenium ecuadorense Stolze, sp. nov.

Rhizoma erectum, paleaceum; paleae 2–4 mm longae, deltato-lanceolatae vel -ovatae, brunneae vel fuscae, conspicue clathratae; folium 20–45 cm longum, 6–15 cm latum, tripinnatum vel sutripinnatum, fasciculatum; petiolus 1–3 cm longus, plerumque brunneus, numquam nitidus; lamina gradatim angustata apicem pinnatifidam vel flagelliformem versus, saepe apice prolificanti, ad basin gradatim angustata; pinnae 34–60-jugae, lanceolato-oblongae, confertae vel imbricatae, patentes, vel pinnae proximales deflexae, sessiles, pinnulis basalibus admodum superpositis supra rachin; venae segmentorum ultimorum simplices; sori in quoque segmento solitarii; indusium delicatum, subintegrum.

TYPE: "Cordillera occidentalis: Río Suquibi ad radices occid. spect. mts. Chimborazzo [Prov. Bolívar, Ecuador], 500 m, in silvis humidis, arborum pedis ornans," *Rimbach 16* [Rosenstock exsicc. no. 10] (US, 2 sheets: 1197005–6; isotypes GH, S, US).

In wet forests, commonly on trunks of trees, very rarely on the forest floor, 100–1400 m, thus far found only in Ecuador.

Plants epiphytic, rarely terrestrial; rhizome stout, erect, provided with deltoid-lanceolate or -obovate, brown or gray-brown scales, these 2–4 mm long, conspicuously clathrate, the lumina large and clear; leaves to 45 cm long, 6–15 cm broad, tripinnate or subtripinnate, fasciculate; petiole 1–3 cm long, terete, dull brown or reddish brown, nonalate, occasionally marginate, glabrous or with scattered, minute, filiform scales; lamina glabrous, thin-herbaceous to membranaceous, dark

FIGS. 1–3. *Asplenium ecuadorense*. FIG. 1. Habit. ×0.5. FIG. 2. Portions of rachis and two pinnae, adaxial side, ×6. FIG. 3. Rhizome scale, ×12.

green, elliptic-attenuate, strongly and gradually reduced to a pinnatifid or flagelliform apex and often with a proliferous tip, strongly and gradually narrowed at base, with 8–18 slightly to greatly reduced pinnae; rachis dark or reddish brown, marginate or narrow-alate; pinnae (30)34–60 pairs, crowded to imbricate, mostly patent, but some proximal ones commonly deflexed, oblong-lanceolate, their margins subparallel for much of their length, sessile, the basal pinnules strongly overlapping the rachis; pinnules 10–20 pairs, cut nearly or quite to the costa into 1–3 pairs of segments, these elliptic or ovate-elliptic, entire (or often the basal acroscopic ones deeply bifid), obtuse or subacute, cuneate at base; veins simple in each ultimate segment, with tips not or slightly enlarged and terminating well short of the segment apex; sori solitary on the vein of each segment; indusium delicate, yellowish or greenish, subentire.

SELECTED SPECIMENS EXAMINED:

ECUADOR: Bolívar: Western Cordillera, western slope of the river Suquibí, 500 m, *Rimbach 29* (topotypes GH, US). **Cotopaxí:** Epiphyte, produces new crowns from a terminal bud. On road from Quevedo to Quito, ca. 500 m, *Haught 2917* (GH, S, UC, US). **Guayas:** Crescit in silv. trop. prop. Puente de Chimbo, 8/1891, *Sodiro 20/47* (P). **Los Ríos:** Epiphytic fern, lightly disturbed forest on hills; Centinela Ridge area, 12.5 km E of Patricia Pilar, 1400 ft, *Hansen et al. 7746* (AAU, MO). **Manabí:** Chone-Santo Domingo Road, near Río La Morena, ca. 15 km NNE of Flavio Alfaro, remnants of seasonal rain forest, ca. 100 m, *Harling & Andersson 18909* (GB). **Pichincha:** Seasonal rain forest, 20 km W of Santo Domingo de los Colorados, 1000 ft, *Cazalet & Pennington 5264* (NY, UC, US). **Tungurahua:** Western Cordillera, W of town of Ambato, 500 m, moist forest region, *Rimbach 640* (F). **Zamora-Chinchipe:** Fallen trees on hilside, on tree trunk, road from Loja to Zamora, km 42, 1400 m, *Dodson & Thien 843* (MO).

The general aspect of this new species is that of *A. rutaceum* in that both have the lamina strongly reduced at the apex and base, with the tip of the rachis often flagelliform and radicant. The pinnae of both are commonly borne at right angles to the rachis and are sessile, with the basal pinnules strongly overlapping the rachis, and the pinna margins parallel for most of their length. In addition, the rhizome scales are gray-brown and conspicuously clathrate. However, *A. ecuadorense* differs obviously from *A. rutaceum* in that the pinnae are much more crowded (often strongly imbricate) and numerous (ca. 35–50 pairs vs. 15–30 pairs), and the petioles and lower rachises are dull brown or reddish brown, vs. castaneous to atropurpureous and highly lustrous in *A. rutaceum*.

Asplenium myriophyllum is the other species with which *A. ecuadorense* might be easily confused. Both are similar in gross morphological characteristics: tripinnate or subtripinnate lamina, strongly reduced to both apex and base; dull (never shiny), usually reddish brown petiole; pinnae sessile, with basal pinnules crowding the rachis. But the new species has gray-brown rhizome scales that are conspicuously clathrate, whereas in *A. myriophyllum* these are castaneous to blackish and only obscurely clathrate (i.e., the lumina are greatly constricted). Also, *A. ecuadorense* pinnae (ca. 35–50 pairs) mostly spread at right angles from the rachis, are crowded to imbricate, and are predominantly oblong, *i.e.* the margins are parallel for most of their length. In comparison, *A. myriophyllum* has fewer pinnae (ca. 18–25 pairs), which are mostly ascending and much less crowded, and are broadest at or near the base, tapering abruptly or gradually to apex.

Three more species came to light during studies on the "Flora of Ecuador" and they are described here.

FIGS. 4–6. *Asplenium oellgaardii*. FIG. 4. Habit, ×0.5. FIG. 5. Apex of leaf, with proliferous tip. ×3. FIG. 6. Central portion of rachis, with several pinnae, ×6.

Asplenium oellgaardii Stolze, sp. nov. Figs. 4–6.

Asplenium trichomanes var. *herbaceum* Sod. Anal. Univ. Quito 8(58):269. 1893 (seors. 145). 1897. TYPE: "In sylv. vulc. Pasochoa. IX/90," *Sodiro s. n.* (not seen; probable isotype US1196744).

Rhizoma parvum, erectum, paleaceum; paleae 1.5–2.5 mm longae, lineari-lanceolatae, attenuatae, nigricantes, obscure clathratae, folium 7–18(22) cm longum, 1.2–2.5 cm latum, pinnatum; petiolus 1.5–4.5 cm longus, brunneus, numquam nitidus, paleis sparsis, tortuosis, filiformibus, castaneis vel nigricantibus; lamina glabra, angustata apicem flagelliformem versus, saepe apice prolificanti; pinnae 10–24-jugae, approximatae vel subimbricatae, patentes vel leviter adscendentes, oblongae, obtusae, ad basin valde inaequilaterales; venae 2–4-jugae, simplices, manifestae vel indistinctae.

TYPE: San Miguel, on margin of paramo between Atantaqui and Hacienda Piñan, Prov. Imbabura, Ecuador, 3420 m, *Wiggins 10333* (UC; isotypes F, US).

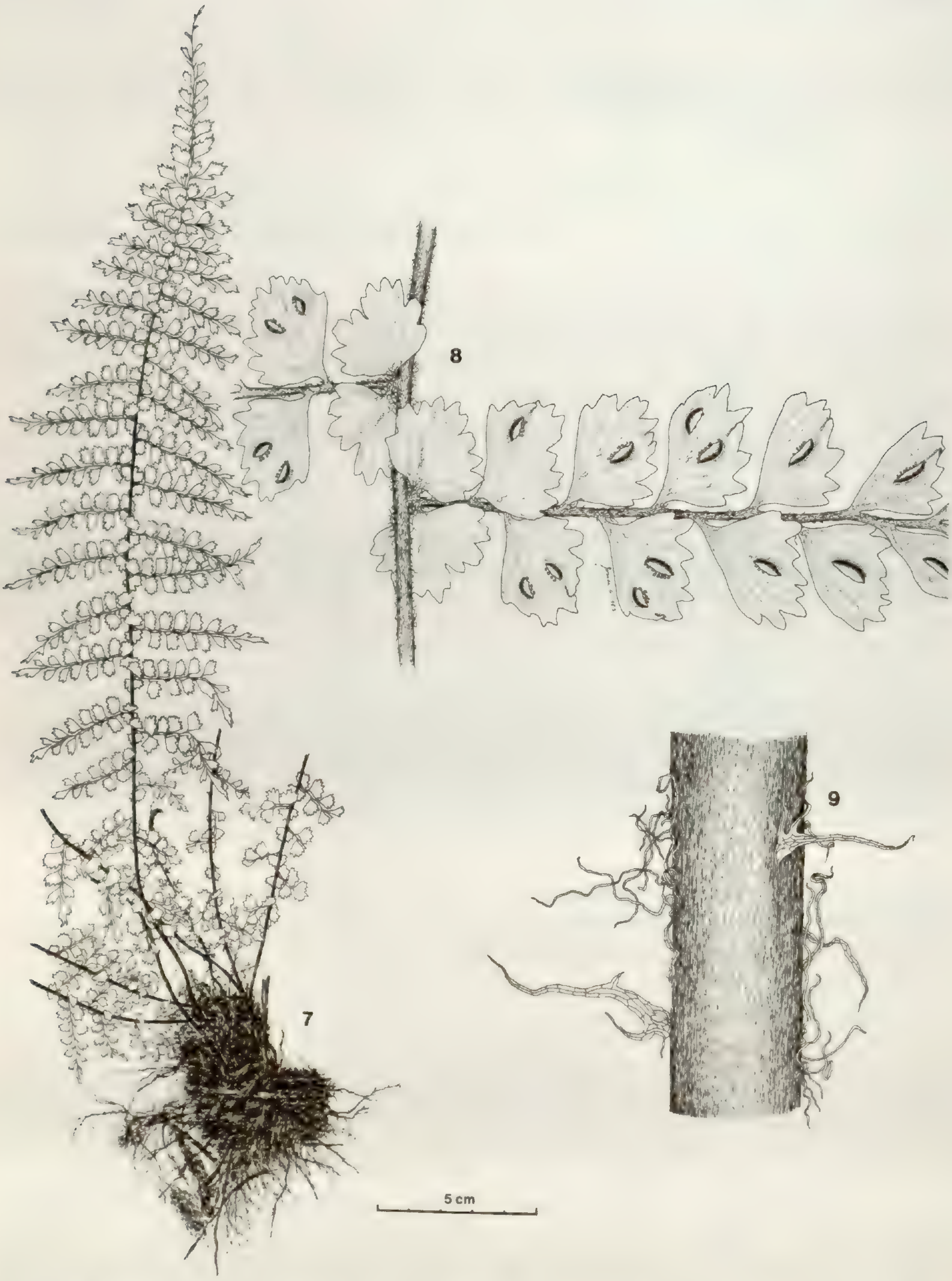
In andine forests, commonly on shaded slopes and banks of quebradas, 2150–3400 m, thus far found only in Ecuador and in one location in Colombia.

Plants terrestrial; rhizome small, compact, erect, provided with linear-lanceolate, attenuate scales, these 1.5–2.5 mm long, blackish, or occasionally with very narrow brownish margins, obscurely clathrate, the lumina small and the walls relatively thick; leaves 7–18(22) cm long, 1.2–2.5 cm broad, pinnate; petiole 1.5–4.5 cm long, 0.5–1.2 mm in diameter, dull reddish to grayish brown, flattened or terete at the base, marginate or narrow-alate at least toward the base of the lamina, provided with scattered, modified, castaneous or blackish, tortuous, filiform scales; lamina essentially glabrous, thin- to firm-herbaceous, narrowly oblong-lanceolate, rather abruptly reduced to a pinnatifid apex or, much more commonly, terminating in a flagelliform, proliferous tip, somewhat to scarcely reduced at the base; rachis marginate to narrowly alate, or very rarely more strongly alate, often provided with a few scattered, dark, filiform, unicostate scales; pinnae 10–24 pairs, 6–15 mm long, 4–8 mm broad, approximate to subimbricate, patent or slightly ascending, short-stalked, oblong, obtuse, strongly inequilateral at the base, truncate acroscopically, narrowly cuneate basiscopically, the margins entire, or more commonly broadly crenate acroscopically; veins distinct to indistinct, 2–4 pairs, simple or the basal acroscopic one 1- or 2-forked; sori 2–6(9) on a pinna, commonly borne nearer to the pinna apex than to the base; indusium yellowish to greenish, 2–4 mm long, linear to narrow oblong, the margin entire.

SELECTED SPECIMENS EXAMINED:

COLOMBIA: Caldas: Clearing, "Pinares," above Salento, 2700–2900 m, *Pennell 9696* (US). **ECUADOR: El Oro:** Along Quebrada, on S-, SW-, and W-facing slopes in Montaña Sichicay, near Cachicarán, tributary to Río Minas Nuevas, above Huertas, E and NE of Paccha, 2135–2285 m, *Steyermark 54117* (F). **Loja:** On shaded bank on upper slopes of Colambo, SE of Gozanama, 2750 m, *Wiggins 10987* (MO, UC). *Correll E-397* (US). Cerro Villanaco, 7–12 km W of Loja, 8000–9000 m, *Wiggins 10987* (MO, UC). *Correll E-397* (US). Cerro "Halo," 2500–3100 m, *Acosta Solis 14061* (F). Ad Cotocollao, 2750 m, *Mille s. n.* (S). Nono, 9/1899, *Sodiro s. n.* (NY). Cotocallao, *Verleysen s. n., pro parte* (UC). **Province unknown:** "In silv. regionis interand." *Sodiro s. n.* (US 1196743, *pro parte*).

As is common with most of Sodiro's new taxa, it is difficult to be certain of authentic type material, but probably US1196744 is an isotype of *A. trichomanes* var. *herbaceum*. This and the other Sodiro specimens cited above apparently were intended for this new variety, but on the species level, the epithet *herbaceum* previously had been used by Fée (1857) and by Baker (1874) for other plants, thus requiring a different epithet. Furthermore, *A. oellgaardii* is not closely related to *A. trichomanes*, which is a fern of temperate regions having a dark and



FIGS. 7–9. *Asplenium subdimidiatum*. FIG. 7. Habit. ×0.5. FIG. 8. Central portion of rachis, with pinna, abaxial side. ×3. FIG. 9. Portion of rachis, with scales. ×25.

lustrous petiole and rachis, a non-proliferous leaf apex, and subequilateral pinna bases. *A. oellgaardii* has dull reddish to grayish brown petioles, strongly inequilateral pinna bases, and the leaf tip is generally proliferous.

This new species has been found in various herbaria also determined as *A. fragile* Presl and as *A. debile* Sod. Leaves of the closely related *A. fragile* may often bear proliferous buds in pinna axils, but rarely, if ever, at the tip of the rachis. Also, the pinnae are irregularly obovate to rhomboid, whereas the pinnae in *A. oellgaardii* are oblong. Less closely related is *A. ruizianum* (syn. *A. congestum* C. Chr., a new name for *A. debile* Sod., *non* Fée, 1869). This differs from *A. oellgaardii* by its fewer pinnae (4–10 pairs). Also, the lamina is equal to or shorter than the petiole and bears no proliferous buds; whereas in *A. oellgaardii* the lamina greatly exceeds the short petiole.

This new species is named in honor of my good friend Benjamin Øllgaard, who not only is coordinating the contributions of pteridophyte treatments for the "Flora of Ecuador," but is actively engaged in field work for the Flora.

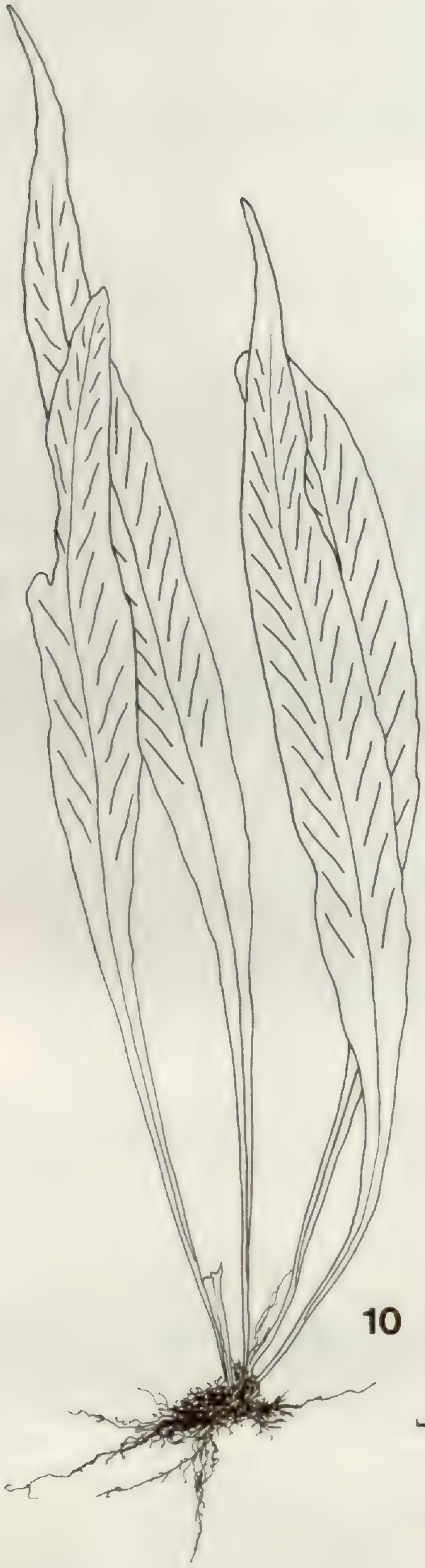
Figs. 7–9.

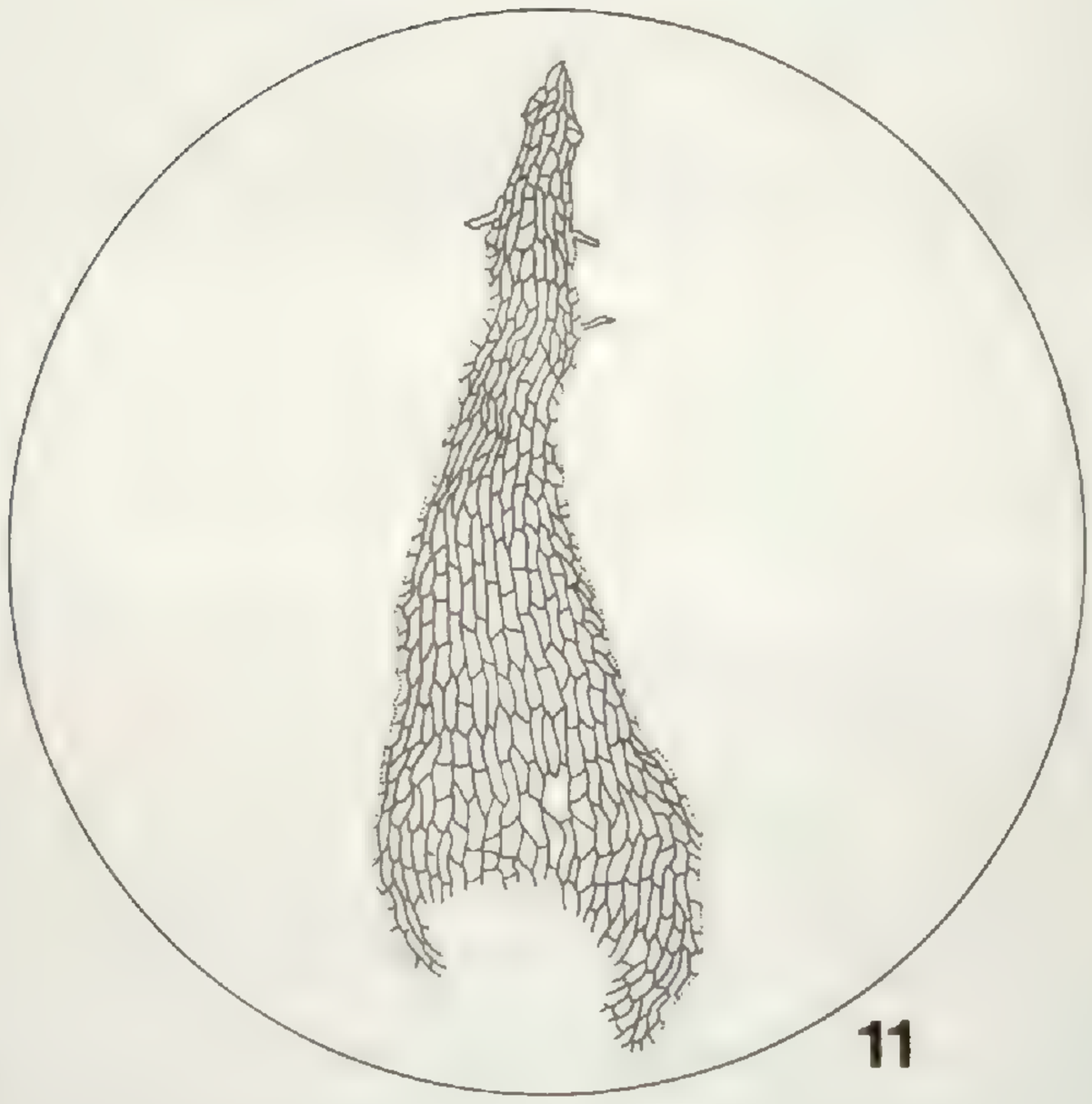
Asplenium subdimidiatum Stolze, sp. nov.

Rhizoma erectum, paleaceum; paleae 1.5–2.5 mm longae, deltato-lanceolatae vel lineares, attenuatae, brunneae, clathratae; folium 18–30 cm longum, 5–8 cm latum, bipinnatum, fasciculatum; petiolus 1.5–3.5 cm longus, obscure brunneus vel nigrescens, paleis usque ad 2 mm longis, abundantibus, tortuosis, filiformibus instructus; lamina gradatim angustata apicem pinnatifidam vel attenuatam versus, non prolifica, ad basin gradatim angustata; pinnae 15–28-jugae, approximatae, lanceolato-oblongae, patentes vel leviter deflexae, sessiles, pinnulis basalibus admodum superpositis supra rachin; pinnulae trapeziformes, subdimidiatae; venae subdichotomae vel subflabelliformes; indusium crassum, brunneolum, nigrescens ubi affixum.

TYPE: Epiphytic. Lagunas de Cyabeno, second lake, situated some 3 km W of the first lake, Prov. Napo, Ecuador, primary forest with some periodically flooded parts, 300 m, 23 Aug. 1981, *Brandbyge, Asanza, Werling & Leth-Nissen 36016*. (AAU). Known only from the type.

Plants epiphytic; rhizome erect, provided with deltoid-lanceolate or linear, attenuate, dark brown scales, these 1.5–2.5 mm long, clathrate, the lumina small but clear; leaves 18–30 cm long, 5–8 cm broad, bipinnate, fasciculate; petiole 1.5–3.5 cm long, terete or subterete, dark brown to blackish, dull or slightly lustrous, nonalate, amply to abundantly provided with linear to filiform scales to 2 mm long, these commonly tortuous and filiform for most of their length, or 3–7 cells broad at base; lamina thin-herbaceous to membranaceous, elliptic-attenuate, strongly and gradually reduced to a pinnatifid or attenuate apex, not proliferous, strongly and gradually narrowed at base, with 4–6 pairs of slightly to greatly reduced pinnae, provided sparsely (at least on costae and veins abaxially) with minute, branched to irregularly stellate, gland-tipped trichomes; rachis dark brown, terete, nonalate, scaly as on the petiole; pinnae 15–28 pairs, approximate, patent to slightly deflexed, oblong-lanceolate, their margins subparallel at least toward the pinna base, sessile, the basal pinnules strongly overlapping the rachis; pinnules 3–6 pairs, subsessile to short-stalked, cuneate and flabelliform or more commonly, trapeziform, subdimidiate, truncate, and strongly produced acroscopically, narrowly cuneate or strongly excised basiscopically, the margins sharply and deeply dentate acroscopically, entire basiscopically; veins forking subdichotomously from at or near the base, vein tips terminating in teeth of the pinnules; sori 1–3 in each pinnule, elliptical, entire, rather thick-textured, brownish, but becoming blackish along the line of attachment.





FIGS. 10, 11. *Asplenium pseudoangustum*. FIG. 10. Habit. ×0.5. FIG. 11. Rhizome scale. ×12.5.

Normally I would choose not to describe a novelty on the basis of a single collection, but this is a very distinctive fern and is not likely to be confused with any other species in the genus.

Two particularly distinctive features of this new species help separate it from most others of the genus: the conspicuous scales of the petiole and rachis and the peculiar, branched trichomes on the veins and costae. The scales are of a type common to species included in sect. *Sphenopteris* by Morton and Lellinger (Mem. New York Bot. Gard. 15: 5. 1966), *i.e.*, dark brown to castaneous, very narrow and usually tortuous, often appearing more like trichomes than scales, clathrate, some of them 3–7 cells broad near the base, yet often attenuate to a single-ribbed apex, and more commonly single-ribbed throughout, the lumina reduced to just a few short, lateral cross walls, but not enclosed. An even more distinctive feature of *A. subdimidiatum* is the inconspicuous indument which sparsely dots the pinnules, particularly on the abaxial surface. Here and there along the veins and occasionally on the costae are scattered, appressed, brownish trichomes which are branched from the point of attachment, the two to several arms often terminating in a slightly enlarged, colorless gland. Admittedly they are tiny (0.1–0.2 mm) and perhaps will go unnoticed except under higher magnification, but to my knowledge they have not been found in other species of *Asplenium*.

The scaly axes and the shape of some of the pinnules are suggestive of *A. cuneatum* Lam., but there the resemblance ends. In the latter species, the lamina is broadest at or near the base, so also are the short-stalked pinnae, and the sori are commonly linear (many times longer than broad). In *A. subdimidiatum*, the lamina is conspicuously narrowed at base, the pinnae have their margins parallel at least toward the base and are quite sessile, with the basal pinnules strongly overlapping the rachis, and the sori are elliptical, usually only about twice as long as broad.

Superficially the new species resembles *A. cristatum* Lam. in the crowded, sessile pinnae and the general aspect of the lamina. But *A. cristatum* has far more pinnules (8–12 vs. 3–6 pairs on larger pinnae), the laminae are not narrowed at base, and the axes are not or scarcely scaly.

Asplenium pseudoangustum Stolze, sp. nov. **Figs. 10–11.**

Rhizoma parvum, erectum vel adscendens, paleaceum; paleae 1.5–3 mm longae, lanceolatae vel ovatae, acutae vel acuminatae, brunneae, clathratae; folium 8–20 cm longum, 1.3–2.5(3) cm latum, sessile vel subsessile, simplex; lamina glabra, firme herbacea, elliptica, acuta vel subacuta, ad basin attenuata, margine integra; sori lineares, recti vel aliquantum arcuati, distantes.

TYPE: Tingo Maria, Prov. Huánuco Peru, 700 m; hillside forest, epiphytic on trunks and branches of small trees, *R. M. & A. F. Tryon 5257* (GH; isotypes F, US).

In deep shade of wet forests, on trunks or branches of trees, 350–1400 m; Ecuador; Peru.

Plants epiphytic; rhizome small, erect to ascending, provided with dark or light brown, clathrate scales, these lanceolate to ovate, acute to acuminate, 1.5–3 mm long; leaves erect, caespitose, sessile or subsessile, simple and unlobed, 8–20 cm long, 1.3–2.5(3) cm broad; petiole essentially lacking; lamina firm-herbaceous to subcarnose, elliptic, apex acute or subacute (very rarely attenuate), long-attenuate at base, the margins entire, the surfaces and midrib glabrous; veins once- or sometimes

twice-forked, obscure, spreading at a 30–45° angle from the midrib; sori straight or somewhat arcuate, well-spaced, elongated, medial between midrib and margin; indusium narrow, elongated, pale green or yellow-green.

SELECTED SPECIMENS EXAMINED:

ECUADOR: Morona-Santiago: Macuma, on the Macuma River, S of Chiquaza, tropical rain forest, ca. 700 m, *van der Werff 659* (GH). **PERU: Cuzco:** Tupitani, Prov. Convención, epiphytic, 2000 ft. *Bües 5450* (US). **Junín:** Pichis trail, Yapas; alt. 1350–1600 m, in dense forest on fallen log, *Killip & Smith 25560* (NY, US). Puerto Bermudez, ca. 375 m, on tree in dense forest, *Killip & Smith 26545* (NY, US). **San Martín:** Entre Aucayacu y Uchiza, margen derecha Río Huallaga, Prov. Mariscal Cáceres, 500–600 m, *Ferreyra 17038* (GH). Palo Blanco al oeste del Puente, Mariscal Cáceres, Tocache Nuevo, 600–700 m, *Schunke 5671* (F, US). Puerto Pizana, Mariscal Cáceres, Tocache Nuevo, 350 m, *Schunke 6951* (F).

A single Ecuadorean collection came to my attention which at first I assumed was a depauperate specimen of *A. serratum* L. or which perhaps represented a range extension for *A. angustum* Swartz. Closer examination of this *Asplenium* with small, undivided laminae proved it was quite distinct from either, and a further search of the Field Museum collections and other herbaria turned up a number of specimens from Peru. Most of these had been determined "*Asplenium angustum* vel aff."

This superficially does resemble *A. angustum* of Colombia, Venezuela, the Guianas, and Brazil (which is perhaps itself merely a variant of *A. serratum*). But there are differences in texture and indument of the lamina, rhizome scales, and soral arrangement. In *A. angustum* the rhizome scales are linear to filiform, castaneous to black, and commonly terminate in a thin, unicostate tip, there are minute, dark, clathrate scales scattered on the midrib of the rather thick lamina, and the sori are crowded and borne at a very acute angle. In *A. pseudoangustum*, the rhizome scales are ovate to lanceolate, lighter in color, with the apex merely acute; the lamina is thinner in texture and lacks scales; and the sori are widely spaced and borne at a less acute angle from the midrib.

REVIEW

USOS DE LOS HELECHOS EN SURAMÉRICA CON ESPECIAL REFERENCIA A COLOMBIA, by María Teresa Murillo P. 156 pp. Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá, 1983.—The introductory third of this well printed paperback book includes a brief history of Colombian botany and a key to the families of pteridophytes found in South America. Numerous beautiful line drawings by Eugenia de Brieva illustrate the families. The main text is an alphabetical list by Latin name of ferns and fern-allies with their uses, as recorded in botanical literature. A brief description of each plant, its vernacular name(s), its distribution in Colombia, and its uses (often including quotations from the literature) are given. Fourteen color habit photographs taken in the field are included. Indices to vernacular and Latin names and a bibliography conclude the volume. This book will be of interest to many botanists, but is especially important to ethnobotanists and pharmacologists.—*D.B.L.*

Frequency of Cyanogenesis in Bracken in Relation to Shading and Winter Severity

I. SCHREINER,* D. NAFUS,* and D. PIMENTEL**

A number of studies have shown that cyanogenic phenotypes of plants are less palatable to, and less damaged by, many herbivores than are acyanogenic phenotypes of the same species (Jones, 1962; Angseesing & Angseesing, 1973; Cooper-Driver & Swain, 1976; Dritschilo et al., 1979; Schreiner et al., 1984). Yet many plant species are polymorphic for cyanogenesis, and the acyanogenic morphs are common (Fikenscher & Hegenauer, 1977). Studies on this polymorphism in *Trifolium repens* and *Lotus corniculatus* have shown that a variety of environmental stresses are more deleterious to cyanogenic plants than they are to acyanogenic ones. In *Trifolium*, low winter temperatures are correlated with low frequencies of plants containing cyanogenic glucoside (Daday, 1954; De Araujo, 1976). However, the correlation between low winter temperatures and a high incidence of acyanogenic plants is poorer for *L. corniculatus* (Jones, 1977). Cyanogenic *Lotus* and *Trifolium* plants were less tolerant of drought (Abbott, 1977; Foulds & Grimes, 1972). In some situations, salt spray may also select more strongly against cyanogenic *Lotus* plants (Keymer & Ellis, 1978). Cooper-Driver (1976) found that Bracken, *Pteridium aquilinum* (L.) Kuhn, was polymorphic for cyanogenesis and that cyanogenic Bracken fronds growing in the shade had higher cyanide levels than those growing in open, sunny habitats (Cooper-Driver et al., 1977). The incidence of cyanogenic and acyanogenic fronds in the two habitats was not measured. In an attempt to follow up on this work, the current study examined the incidence of cyanogenic and acyanogenic fronds in open and shady habitats. A survey was also made to determine if there was any correlation between winter severity and the incidence of cyanogenesis in Bracken stands.

MATERIALS AND METHODS

The relationship of habitat to the incidence of cyanogenesis in Bracken was examined by surveying fronds within a 20 km radius of Ithaca, New York, primarily in the Connecticut Hill Wildlife Management Area. Bracken stands were classified as shady if a closed tree canopy shaded all the fronds. Stands growing in open fields were classified as sunny, and stands growing at the edge of woodlands were classified as partially shaded. Fronds were collected by walking across the longest dimension of the stand and collecting a frond every meter. Ten fronds were sampled from stands of less than 100 m^2, and 20 fronds were taken from larger stands. The fronds were collected in late May and early June.

To test for cyanide levels in the Bracken fronds, 6 mm from the end of one of the lowest pinnae of the fronds was removed (about 0.2 g plant material). The sample was placed in a glass vial and crushed with a glass rod to disrupt the tissue. If both cyanogenic glucoside and one or more cyanide-releasing enzymes were present in a frond, this disruption would cause them to come into contact and release cyanide ions.

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TABLE 1. DISTRIBUTION OF CYANOGENIC AND ACYANOGENIC BRACKEN FRONDS UNDER VARIOUS LIGHT CONDITIONS.

A. Percentage of cyanogenic fronds in various habitats

Type of frond	*Open-sunny* (170 fronds)	*Partial shade* (150 fronds)	*Shade* (140 fronds)
HCN –	82%	79%	66%
HCN +	18	21	34

B. Levels of cyanide in the cyanogenic fronds above

Amount of HCN	*Open-sunny* (31 fronds)	*Partial shade* (31 fronds)	*Shade* (48 fronds)
Low	35%	13%	8%
Medium	48	61	58
High	16	26	33

After the frond was crushed, a strip of filter paper (3.5 cm × 0.5 cm) impregnated with 0.5 ml picric acid solution was inserted and the vial stoppered (Dawson, 1941). After one hour, the paper was examined. If it had turned purplish brown, the frond was scored as highly cyanogenic. If the paper had turned orange within the hour, the frond was scored as medium cyanogenic. The vials containing papers which showed no color change were kept overnight. If the paper had turned orange within 24 hours, the cyanide level of the frond was scored as low. If there was no change in the color of the filter paper within a 24 hour period, the frond was scored as acyanogenic, lacking either the glucoside, the enzyme(s), or both, so that cyanide ions were not released.

The relationship between the incidence of cyanogenesis in Bracken and winter severity was investigated by sampling Bracken stands about every 150 km along a 1000 km transect from Ithaca, New York southwards towards Fayetteville, North Carolina. Every 150 km, 20 Bracken stands were found along rural roads. Five fronds were taken from each stand. Cyanogenesis in the fronds was measured as described previously, except that only the release of cyanide ions was recorded in these samples, with no attempt to quantify the amounts. Locations south of Washington, DC were sampled in the first week of May, 1978, and those to the north, in mid-June.

RESULTS

Two-thirds of the large Bracken stands and half of the small ones sampled contained both cyanogenic and acyanogenic fronds, indicating that at least two ecotypes of Bracken were present. Differences in the appearance of the fronds suggested that in many cases, more than two ecotypes were present.

Fronds from shaded stands were nearly twice as likely to be cyanogenic as were fronds from sunny stands (34% vs. 18%, *Table 1A*). The raw data were analyzed using a Chi-square test, and the difference was significant at the 0.025 level. There was also a 90% probability (Chi-square) that fronds growing in the shade released more cyanide than did those growing in the sun *(Table 1B)*.

Differences in winter severity did not seem to be related to the incidence of cyanogenesis in Bracken populations *(Fig. 1)*. About 25% of the fronds were cyanogenic in both the northernmost and the southernmost samples, whereas the intermediate sites had lower frequencies.

FIG. 1. Percentage of cyanogenic Bracken fronds (large numbers) at sites in the eastern United States in relation to winter severity expressed as the average minimum temperature for February (small numbers) at the nearest weather station (U.S. Dept. of Commerce, 1979, pp. 1–2).

DISCUSSION

Cyanogenesis in Bracken was significantly associated with habitat. Fronds growing in shaded stands were twice as likely to be cyanogenic as were fronds growing in open fields. Cyanogenic fronds growing in the shade may also have released more cyanide ions than cyanogenic fronds growing in the sun (90% probability), even though fronds in the woods came up one to two weeks earlier than those growing in open areas. Note, however, that older fronds would be expected to have lower cyanide levels, as the quantity of cyanide is highest in the fiddleheads and decreases rapidly as the fronds age (Greshoff, 1908; Moon & Raafat, 1951; Cooper-Driver et al., 1977; Schreiner, et al., 1984). Our results agree with those of Cooper-Driver et al. (1977), who also reported higher levels of cyanide in fronds growing in shaded sites than in those growing in the open.

The earlier appearance of Bracken fronds in shaded habitats than in sunny habitats was unexpected since open areas generally warm up earlier in the spring (Geiger, 1966). Hellum and Zahner (1966) suggested that in Michigan, early emerging Bracken fronds were likely to be damaged by late frosts while still in the litter layer, so that plants in open areas were set back compared to those in woodlands. It seems probable that the same is true in rural New York.

One possible cause for the different frequency of cyanogenic fronds in wooded and open areas is a difference in fertility between the sites. Cyanogenesis in Bracken has been found to be markedly enhanced by application of urea fertilizer (J.H. Lawton, pers. comm.). The Connecticut Hill area appears to have infertile soils, but perhaps the Bracken growing in wooded areas get some additional nutrients from the litter of the trees shading them.

Lawton (pers. comm.) has found that in Britain moths mining the young croziers appear to induce cyanogenesis in the vicinity of their mines. In rural New York, crozier-mining lepidopterans were most common in shaded sites (Schreiner, 1980). However, no correlation between the presence of mines and cyanogenesis was observed. (Schreiner et al., 1984).

Cyanogenesis in Bracken did not appear to be related to overall winter severity, as the incidence of cyanogenic plants was lower at the intermediate sites than at the most southern and northern ones. This contrasts with the results found for *T. repens* (Daday, 1954; De Araujo, 1976), but not with those observed for *L. corniculatus* (Jones, 1977).

Partial funding of this research was provided by NSF Grant DEB-8010912. We wish to thank Dr. Clive G. Jones for valuable comments.

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FLORA OF ECUADOR 14(4). POLYPODIACEAE—THELYPTERIDOIDEAE, by Alan R. Smith. Flora of Ecuador 18:1–148. 1983.—*Thelypteris* is among the largest genera of ferns in the New World tropics and has a large concentration of species in the Andean countries. Because many species of *thelypteris* are widespread, this paper will be helpful from Costa Rica through Bolivia. Smith treats this genus in the broad sense, and includes 100 species for Ecuador. He thinks another 25 species may remain to be discovered. His treatment divides the genus into subgenera *Macrothelypteris*, *Goniopteris*, *Meniscium*, *Amauropelta*, *Steiropteris* (including *Glaphyropteris*), and *Cyclosorus*. I have used the keys in all the subgenera, and find that all of them work well. The species and infraspecific taxa are arranged alphabetically within each subgenus. Each has a synonymy, description, citation of specimens, and notes. Several new species are described and illustrated, and some new combinations are made. For students of the genus, it would have been helpful if the sections of subg. *Amauropelta* had been included with the species name, but constraints of format probably did not permit this. The information is often given in the notes. The paper includes an index and a map of the provinces of Ecuador, both welcome features. The paper may be purchased from the Swedish Research Councils Publishing House, Box 6710, S-11385 Stockholm, Sweden.—*D.B.L.*

New Combinations and Some New Names in Ferns

DAVID B. LELLINGER*

The forthcoming publication of microfiches and an index of the pteridophyte types in the U.S. National Herbarium (US) requires that the following combinations and new names be made.

Asplenium radicans var. alloeopteron (Kunze ex Klotzsch) Lellinger, comb. nov.

Asplenium alloeopteron Kunze ex Klotzsch, Linnaea 20:353. 1847. SYNTYPES: Guyana, *Schomburgk 1150* (LZ destroyed; isotype B not seen photo 9509[1]), and Guyana, *Schomburgk 1206* (LZ destroyed; isotype B not seen photo 9508 fragm US).

Campyloneurum angustipaleatum (Alston) M. Meyer ex Lellinger, comb. nov.

Polypodium angustipaleatum Alston, J. Bot. Brit. & For. 77:346. 1939. TYPE: Vicinity of Cochabamba, Depto. Cochabamba, Bolivia, *Bang 1288* (BM not seen; isotype US).

Ctenitis aripensis (C. Chr. & Maxon in Maxon) Lellinger, comb. nov.

Dryopteris aripensis C. Chr. & Maxon in Maxon, J. Washington Acad. Sci. 14:143. 1924. TYPE: Heights of Aripo, Trinidad, *Britton & Freeman 2349* (US).

Ctenitis haitiensis (Brause) Lellinger, comb. nov.

Dryopteris subincisa var. *haitiensis* Brause, Ark. för Bot. 17(7):67. 1922. TYPE: Ma Blanche, Morne de la Hotte, Haiti, ca. 1400 m, *Ekman 556* (B not seen fragm & photo US).

Ctenitis paranaensis (C. Chr.) Lellinger, comb. nov.

Dryopteris falciculata var. *paranaensis* C. Chr. Danske Vidensk. Selsk. Skr. VII, 10(2):92. 1913. TYPE: Villa Nova, near the Rio Negro, Est. Paraná, Brazil, *Annies* [*Ros. Fil. Austrobras. Exs. 79*] (S not seen; isotype US).

Ctenitis protensa var. dicksonioides (Fée) Lellinger, comb. nov.

Aspidium dicksonioides Fée, Crypt. Vasc. Brés. 1:143. 1869. TYPE: Near S. Gabriel de Cachoeria, Rio Vaupes, Est. Amazonas, Brazil, *Spruce 2129* (P or RB not seen; isotypes BM not seen, US).

Ctenopteris cryptosora (C. Chr.) Lellinger, comb. nov.

Polypodium decipiens Mett. ex Kuhn, Linnaea 36:129. 1869, *non* Hooker (1862), *nom. illeg.* TYPE: G. Lukambang, Borneo, *Korthals 171* (L not seen photo 844).

Polypodium cryptosorum C. Chr. Ind. Fil. 520. 1906. TYPE: A renaming of *Polypodium decipiens* Mett. ex Kuhn, and so based on the type of that name.

Culcita novae-guineae (Rosenst.) Lellinger, comb. nov.

Davallia novae-guineae Rosenst. Repert. Sp. Nov. Fedde 5:36. 1908. TYPE: Mt. Gelu, New Guinea, 1700 m, *Werner* [*Ros. Fil. Novoguin. Exs. 45*] *73* (B not seen; isotype US).

Cyathea atahuallpa (Tryon) Lellinger, comb. nov.

Sphaeropteris atahuallpa Tryon, Rhodora 74:442, *f.5–8*. 1972. TYPE: E side of Cerros Calla Calla above Balsas on road to Leimebamba, Depto. Amazonas, Peru, 3000–3100 m, *Wright 6922* (GH not seen; isotype US).

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[1]Here and elsewhere the word "photo" followed by a number refers to the numbered series of photographs taken by C. V. Morton and distributed from the U.S. National Museum.

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Cyathea bradei (Windisch) Lellinger, comb. nov.

Sphaeropteris bradei Windisch, Bradea 1:372, *f. 1, 2, 9.* 1973. TYPE: Base of Cerro Mitu, Comis. Vaupés, Colombia, *Schultes, Raffauf & Soejarto 24229* (GH not seen).

Cyathea intramarginalis (Windisch) Lellinger, comb. nov.

Sphaeropteris intramarginalis Windisch, Bradea 1:373, *t. I, f. 5; t. II, f. 3, 4, 10.* 1973. TYPE: Sarvén-tepuí, Edo. Bolívar, Venezuela, 1750 m, *Wurdack 34154* (GH not seen; isotypes NY not seen, US).

Cyathea lockwoodiana (Windisch) Lellinger, comb. nov.

Sphaeropteris lockwoodiana Windisch, Bradea 2:57. 1976. TYPE: Cerro Chiribiquete, Rio Macaya, Río Apaporis, Comis. Vaupés, Colombia, *Schultes 5635* (GH not seen; isotype US).

Cyathea parianensis (Windisch) Lellinger, comb. nov.

Sphaeropteris parianensis Windisch, Bradea 2:58, *f. 5, 8.* 1976. TYPE: Cerro Patao, N of Puerto de Hierro, Peninsula de Paria, Edo. Sucre, Venezuela, 800–825 m, *Steyermark & Agostini 91129* (GH not seen; isotypes US, VEN not seen).

Cyathea sipapoensis (Tryon) Lellinger, comb. nov.

Sphaeropteris sipapoensis Tryon, Rhodora 74:441, *f. 1–4.* 1972. TYPE: Intermediate Camp, Cerro Sipapo (Paráque), Terr. Amazonas, Venezuela, *Maguire & Politi 28765* (NY; isotype GH).

Diplazium subquadripinnatum (Copel.) Lellinger, comb. nov.

Athyrium subquadripinnatum Copel. Occ. Pap. Bishop Mus. 14:61, *t. 14.* 1938. TYPE: Moerai, Rurutu, Austral Islands, 10 m, *H. St. John 16640* (BISH not seen; isotype US).

Diplazium tenuifolium (Copel.) Lellinger, comb. nov.

Athyrium tenuifolium Copel. Phil. J. Sci. 40:302. 1929. LECTOTYPE (chosen here): San Ramon, Zamboanga, Mindanao, Philippines, *Copeland Pterid. Phil. Exs. 198* (MICH, 2 sheets not seen; isolectotype US). Copeland cited three syntypes instead of designating a holotype in describing *A. tenuifolium*. According to M. G. Price (pers. comm.), Copeland marked as type the specimen chosen here as lectotype.

Gleichenia angusta (Klotzsch ex Sturm in Mart.) Maxon ex Lellinger, comb. nov.

Mertensia angusta Klotzsch ex Sturm in Mart. Fl. Bras. 1(2):225. 1859. TYPE: Brazil, *Sellow* (B not seen).

Gleichenia boliviensis (Maxon & Morton) Lellinger, comb. nov.

Dicranopteris boliviensis Maxon & Morton, Bull. Torrey Bot. Club 66:44. 1939. TYPE: Cocopunco, Bolivia, 3000 m, *Tate 351* (NY; isotype US).

Gleichenia peruviana (Maxon) Morton ex Lellinger, comb. nov.

Dicranopteris peruviana Maxon, Amer. Fern J. 33:133. 1943. TYPE: Playapampa, Depto. Huánuco, Peru, ca. 2700 m, *Macbride 4510* (F; isotype US).

Glyphotaenium insidiosum (Slosson) Lellinger, comb. nov.

Polypodium insidiosum Slosson, Bull. Torrey Bot. Club 39:287, *t. 23, f. 4–8.* 1912. TYPE: Near Camp La Gloria, S of Sierra Moa, Pcia. Oriente, Cuba, *Shafer 8043* (NY; isotype US).

Glyphotaenium integrum (Lellinger & Morton) Lellinger, comb. nov.

Enterosora integra Lellinger & Morton, Acta Bot. Venez. 2:123. 1968. TYPE: Summit of the SE part of the NW arm of Auyán-tepuí, Edo. Bolívar, Venezuela, 1850 m, *Steyermark 93415* (US).

Glyphotaenium nesioticum (Maxon) Lellinger, comb. nov.

Polypodium nesioticum Maxon, Smiths. Misc. Coll. 47:410. 1905. TYPE: Vicinity of Vinegar Hill, Portland Parish, Jamaica, 1200 m, *Maxon 2773* (US).

Grammitis allosuroides (Rosenst.) Lellinger, comb. nov.

Polypodium allosuroides Rosenst. Meded. Rijks Herb. Leiden 19:16. 1913. TYPE: Lagodos Valley, Bolivia, 4000 m, *Herzog 2373* (S not seen; isotype US).

Grammitis angustipes (Copel.) Lellinger, comb. nov.

Ctenopteris angustipes Copel. Philip. J. Sci. 84:404. 1956. TYPE: El Silencio, Yanaconas, Depto. El Valle, Colombia, 1900–2200 m, *Killip & Garcia 33843 (US).*

Grammitis basalis (Maxon) Lellinger, comb. nov.

Polypodium basale Maxon, Amer. Fern J. 52:110. 1962. TYPE: Near Puyo, Pcia. Pastaza, Ecuador, 400 m, *Mexia 6930* (US).

Grammitis buesii (Maxon) Lellinger, comb. nov.

Polypodium buesii Maxon, Contr. Gray Herb. 165:72. 1947. TYPE: Cerro Chuyapí, Depto. Cuzco, Peru, 2400 m, *Buës A45* (US).

Grammitis chaseae (Copel.) Lellinger, comb. nov.

Ctenopteris chaseae Copel. Philip. J. Sci. 84:416, *t. 5*. 1956. TYPE: Serra do Caparao, Est. Espíritu Santo, Brazil, ca. 2100 m, 27 Nov 1929, *Chase* (US).

Grammitis ciliolepis (C. Chr.) Lellinger, comb. nov.

Polypodium ciliolepis C. Chr. Ark. för Bot. 20A(7):21. 1926. TYPE: El Chaco Village, Pcia. Sur Yungas, Depto. La Paz, Bolivia, *Asplund 1501* (presumably C not seen fragm US).

Grammitis congesta (Copel.) Lellinger, comb. nov.

Ctenopteris congesta Copel. Philip. J. Sci. 84:397, *t. 3*. 1956. TYPE: Loma Grande, La Convención, Peru, 13000–14000 ft, *Buës 2172* (US).

Grammitis fendleri (Copel.) Lellinger, comb. nov.

Ctenopteris fendleri Copel. Phil. J. Sci. 84:463. 1956. TYPE: A renaming of *Polypodium radicale* Moritz ex Hieron., and so based on the type of that name.

Polypodium radicale Moritz ex Hieron. Bot. Jahrb. Engler 34:511. 1904, *non* Moritz ex Baker, 1867. TYPE: Near Colonia Tovar, Edo. Aragua, Venezuela, *Fendler 215* (B not seen; isotype US).

Grammitis humilis (Mett. in Tr. & Planch.) Lellinger, comb. nov.

Polypodium humile Mett. in Tr. & Planch. Ann. Sci. Nat., Paris, V, 2:251. 1863. TYPE: Chapinerro, Depto. Cundinamarca, Colombia, 2700 m, *Lindig 137* (K not seen photo US: isotype US).

Grammitis kegeliana (Kunze) Lellinger, comb. nov.

Polypodium kegelianum Kunze, Linnaea 21:210. 1848. TYPE: Sornaukreek, Suriname, *Kegel 1072* (GOET not seen).

Grammitis killipii (Copel.) Lellinger, comb. nov.

Xiphopteris killippi Copel. Amer. Fern J. 42:105, *t. 10*. 1952. TYPE: San Antonio, W of Cali, near summit of Cordillera Occidental, Depto. El Valle, Colombia, 1900–2350 m, *Killip & Garcia 33887* (US).

Grammitis longipinnata (Copel.) Lellinger, comb. nov.

Ctenopteris longipinnata Copel. Philip. J. Sci. 84:459, *t. 12*. 1956. TYPE: Cabecera del Koribeni, Alta Huallaga, Depto. Huánuco?, Peru, 9300 ft, *Buës 1952* (US).

Grammitis maxoniana Lellinger, nom. nov.

Polypodium flexuosum Maxon, Contr. U. S. Natl. Herb. 17:597, *t. 42*. 1916, *non Grammitis flexuosa* Humb. & Bonpl. (1816) [=*Eriosorus flexuosus* (H.B.K.) Copel.].

Ctenopteris flexuosa (Maxon) Copel. Phil. J. Sci. 84:434. 1955.

Grammitis mayoris (Rosenst.) Lellinger, comb. nov.

Polypodium mayoris Rosenst. Mém. Soc. Sci. Nat. Neuchatel 5:53, *t. 4, f. 6*. 1912. TYPE: Páramo del Ruiz, Depto. Caldas, Colombia, ca. 3700 m, *Mayor 69* (S not seen; isotype US).

Grammitis melanotricha (Baker in im Thurn) Lellinger, comb. nov.

Polypodium melanotricha Baker in im Thurn, Timehri 5:216. 1886. TYPE: Guyana, *im Thurn 125* (K not seen; isotype fragment US).

Grammitis mortonii (Copel.) Lellinger, comb. nov.

Xiphopteris mortonii Copel. Amer. Fern J. 42:97, *t. 8*. 1952. TYPE: Crest of the Sierra Maestra between Pico Turquino and La Bayamesa, Pcia. Oriente, Cuba, 1350 m, *Morton & Acuña 3547* (US).

Grammitis perpusilla (Maxon) Lellinger, comb. nov.

Polypodium perpusillum Maxon, Contr. U. S. Natl. Herb. 17:409. 1914. TYPE: Serra de Caraça, Est. Minas Gerais, Brazil, March 1892, *Ule* (US).

Grammitis shaferi (Maxon) Lellinger, comb. nov.

Polypodium shaferi Maxon, Contr. U. S. Natl. Herb. 17:410. 1914. TYPE: Camp La Gloria, S of Sierra Moa, Pcia. Oriente, Cuba, *Shafer 8071* (US).

Grammitis williamsii (Maxon) Lellinger, comb. nov.

Polypodium williamsii Maxon, Contr. U. S. Natl. Herb. 17:547, *t. 34*. 1916. TYPE: Near Apolo, Depto. La Paz, Bolivia, 5000 ft, *Williams 1167* (US).

Microgramma acuminata (Fée) Lellinger, comb. nov.

Drynaria acuminata Fée, Crypt. Vasc. Brés. 1:122, *t. 37, f. 3*. 1869. TYPE: Vicinity of Barra [Manaus], Prov. Rio Negro [Est. Amazonas], Brazil, *Spruce* in 1850–51 (RB not seen). [Mickel and de la Sota (pers. comm.) indicate that Fée's epithet is the oldest one for this species, which had been known as *Polypodium loretense* Maxon].

Microgramma latevagans (Maxon & C. Chr. in Maxon) Lellinger, comb. nov.

Polypodium latevagans Maxon & C. Chr. in Maxon, Proc. Biol. Soc. Washington 52:120. 1939. TYPE: Unduavi, Depto. La Paz, Bolivia, 2400 m, *Rusby 361* (US; isotype NY not seen).

Microgramma recreense (Hieron.) Lellinger, comb. nov.

Polypodium recreense Hieron. Bot. Jahrb. Engler 34:537. 1904. LECTOTYPE (chosen here): Near El Recreo, Pcia. Manabí, Ecuador, *Eggers 15838* (US; isolectotype B not seen).

Microgramma tuberosa (Maxon) Lellinger, comb. nov.

Polypodium tuberosum Maxon, Amer. Fern J. 33:135. 1943. TYPE: Vicinity of La Chonta, Pcia. Oro, Ecuador, *Rose, Pachano & Rose 23468* (US).

Pecluma camptophyllaria var. lachnifera (Hieron.) Lellinger, comb. nov.

Polypodium lachniferum Hieron. Bot. Jahrb. Engler 34:515. 1904. LECTOTYPE: Mt. Tungurahua, Pcia. Tungurahua, Ecuador, *Lehmann 458* (B not seen; isolectotypes LE not seen, US), chosen by A. M. Evans (Ann. Missouri Bot. Gard. 55:254. 1968).

Pecluma eurybasis var. glabrescens (Rosenst.) Lellinger, comb. nov.

Polypodium lachniferum var. *glabrescens* Rosenst. Repert. Sp. Nov. Fedde 11:57. 1912. TYPE: Unduavi, North Yungas, Depto. La Paz, Bolivia, *Buchtien 2770* (S not seen; isotype US).

Pecluma eurybasis var. villosa (Evans) Lellinger, comb. nov.

Polypodium eurybasis var. *villosum* Evans, Ann. Missouri Bot. Gard. 55:245, *f. 19*. 1968. TYPE: Above Bogotá just N of the mouth of Quebrada El Obispo, Depto. Cundinamarca, Colombia, 2700 m, *Fosberg 19688* (US).

Pecluma ptilodon var. robusta (Fée) Lellinger, comb. nov.

Polypodium robustum Fée, Crypt. Vasc. Brés. 1:92. 1869. TYPE: Rio de Janeiro, Est. Rio de Janeiro, Brazil, *Glaziou 2407* (presumably P not seen fragm US).

Pleopeltis pleolepis (Maxon & Copel. in Copel.) Lellinger, comb. nov.

Polypodium pleolepis Maxon & Copel. in Copel. Univ. Calif. Publ. Bot. 19:293, *t. 46*. 1941. TYPE: Barranca del Rubelcruz, Depto. Alta Verapaz, Guatemala, 3000 ft, *von Tuerckheim 673* (US).

Polypodium mckeei (Tindale) Lellinger, comb. nov.

Dictymia mckeei Tindale, Amer. Fern J. 50:122. 1960. TYPE: Road to l'Hermitage, Nouméa District, New Caledonia, 400 m, *McKee 2126* (NSW; isotype US).

Polystichopsis cubensis (Kuhn) Lellinger, comb. nov.

Aspidium cubense Kuhn, Linnaea 36:108. 1869. TYPE: Cuba, *Wright 1099* (B not seen; isotype US).

Thelypteris ekmanii A. R. Smith ex Lellinger, nom. nov.

Dryopteris reducta C. Chr. K. Svenska Vetens.-Akad. Handl. III, 16(2):18, *t. 2, f. 1–3*. 1937, *non Thelypteris reducta* Small (1938). TYPE: Valle Nuevo, Pcia. La Vega, Dominican Republic, ca. 2400 m, *Ekman H13839* (C not seen; isotype US).

Thelypteris ireneae (Brade) Lellinger, comb. nov.

Dryopteris ireneae Brade, Sellowia 17:57, *f. 4*. 1965, as "*irenae*." TYPE: Estrada do Contôrno, Serra das Araras, Est. Rio de Janeiro, Brazil, 800 m, *Pabst 5609* (HB; isotype US).

Thelypteris scabra (Presl) Lellinger, comb nov.

Polypodium scabrum Presl, Del. Prag. 1:169. 1822. TYPE: Brazil, without collector (PR not seen).

I wish to thank Alan R. Smith and Michael G. Price for their helpful comments on this paper.

GAULTERIO LOOSER (1898–1982)

Gaulterio Looser was born in Santiago, Chile of Swiss parentage on 4 September 1898. He was an industrialist and an engineer and owned a factory that made agricultural implements. Some of the manufacturing machinery was of his own design. He joined the American Fern Society in 1928 and started to publish papers on the pteridophytes of Chile shortly thereafter. He was made an honorary member of the Society in 1949. His herbarium, containing about 8,000 specimens, was given for the most part to the Conservatoire et Jardin Botaniques, Geneva, Switzerland. He was a Doctor Honoris Causa of the Universidad Católica de Chile and of a Swiss university. His interests and scientific output were broad; he published over 200 papers on ferns, archeology, anthropology, flowering plants, biography, phytogeography, ecology, and geology. He died in Santiago on 22 July 1982.—*From material provided through the kindness of Dr. Clodomiro Marticorena.*

SHORTER NOTES

EQUISETUM RAMOSISSIMUM IN LOUISIANA.—In a recent article (Hauke, R. L. 1979. Amer. Fern J. 69:1–5) I reported the occurrence of *Equisetum ramosissimum* Desf. in North America, from one locality in North Carolina and another in Florida. Dr. A. Murray Evans, of the University of Tennessee, who had sent me the North Carolina specimen of *E. ramosissimum* wrote me in February 1982 about a collection of *Equisetum* from Louisiana that he had noted "looks just like the NC specimen." Since the North Carolina specimen turned out to be *E. ramosissimum*, he suggested I look at this one also.

The specimen in question (Point Coupee Parish, locally common in loose sand near river, Morganza Spillway, St. Hwy 1, west of New Roads, La., 30 Sept 1962, *C. A. Brown & B. B. Exner 17610*, LSU 000056) looked to me like *E.* × *ferrissii*, but a scanning electron micrograph of the surface was needed to be certain. The SEM shows clearly that the silica micromorphology is not that of *E.* × *ferrissii*, but is consistent with that of *E. ramosissimum* or *E. laevigatum*. Anatomically, the stem has both the carinal and the vallecular collenchyma prominent, a feature of *E. ramosissimum*, but not of *E. laevigatum*. Also, the rows of stomata are occasionally doubled, a character of *E. ramosissimum*. Hence, this specimen appears to document the presence of *Equisetum ramosissimum* in Louisiana, an addition to the previous records of that species in North America.—*Richard L. Hauke, Dept. of Botany, University of Rhode Island, Kingston, RI 02881.*

THREE NEW COMBINATIONS IN LOXOGRAMME.—As a result of my annotating many specimens of *Loxogramme* in different herbaria with the following names, I consider it expedient to publish them in advance of a treatment of the genus as a whole:

Loxogramme abyssinica (Baker) Price, comb. nov.

Gymnogramma abyssinica Baker, Syn. Fil., ed. 2: 517. 1874. TYPE: Gerra, Abyssinica, *Schimper 1445* (K).

Loxogramme cuspidata (Zenker) Price, comb. nov.

Grammitis cuspidata Zenker, Plantae Indicae 1: *t.* 2. 1835. TYPE: Near Utacamund, Nilgiris, South India, *Rev. B. Schmid* (not seen; isotypes BR, E, L. P).

Loxogramme wallichiana (Hooker) Price, comb. nov.

Selliguea wallichiana Hooker, Icon. Pl. 3: *t. 204*. 1840. LECTOTYPE (chosen here): Penang, Malaya, *Wallich 10* (K). The other syntype is Penang, Malaya, *Lady Dalhousie* (K).

M. G. Price, Herbarium, North Univ. Bldg., University of Michigan, Ann Arbor, MI 48109.

NOTES ON NORTH AMERICAN FERNS, II.—Since the publication of the first paper in this series (Amer. Fern. J. 71:90–94), I have found a nomenclatural tangle in one *Dryopteris* hybrid and two more combinations that need to be made:

Adiantum pedatum subsp. subpumilum (Wagner in Wagner & Boydston) Lellinger, comb. & stat. nov.

Adiantum pedatum var. *subpumilum* Wagner in Wagner & Boydston, Canad. J. Bot. 56:1727, *f. 1*. 1978. TYPE: South of Orchard Point, Brooks Peninsula, NW Vancouver Island, British Columbia, Canada, *Pojar & Boas 770191* (MICH; isotypes UBC, V).

This subspecies, known in nature only from Vancouver Island, surely is at least as distinct from subsp. *pedatum* as are subsp. *aleuticum* and the newly described subsp. *calderi* Cody (Rhodora 85:93, *f. 1*. 1983) from Quebec, Newfoundland, and Vermont, with a few outliers along the coast of the northwestern United States.

Dryopteris ×slossoniae Wherry ex Lellinger, sp. nov.

Aspidium cristatum × *marginale* Davenp. Bot. Gaz. 19:494. 1894. AUTHENTIC SPECIMENS: Boxford, Newbury, and Merrimac, Essex County, Massachusetts, *Raynal Dodge* in 1892 (GH ex Herb. Davenport none seen; duplicates US and presumably elsewhere).

Dryopteris cristata × *marginalis* Davenp. Bot. Gaz. 19:497. 1894, *nom. provis. et illeg.*

Nephrodium cristatum × *marginale* Davenp. Bot. Gaz. 19:497. 1894, *nom. provis. et illeg.*

Lastrea cristata × *marginalis* Davenp. Bot. Gaz. 19:497. 1894, *nom. provis. et illeg.*

Nephrodium slossonae Hahne, Allg. Bot. Zeitschr. 10:103. 1904, *nom. nud.*

Dryopteris ×slossonae (Hahne) Wherry, Bartonia 21:15. 1942, *nom. nud.*

Plant hybrida inter *D. cristatam* et *D. marginalem* posita; ex *D. cristata* in rhizomatis erectis laminis latioribus et ad apicem acuminatis et pinnis acuminatis differt; ex *D. marginali* in laminis pallidioribus soris submarginalibus et sporis abortivis differt.

TYPE: Boxford, Essex County, Massachusetts, Aug 1893, *G. E. Davenport 4* (US).

The original publication of the epithet honoring the morphologist Margaret Slosson was by Hahne in a paper on fern hybrids; Hahne listed the hybrid formulae known to him, mostly from Europe, along with their corresponding binomials. In those cases where no binomials had been published, he proposed them, all as *nomina nuda*. Because there is no indication that Hahne knew of Davenport's paper describing *Aspidium cristatum* × *marginale*, or of Slosson's (Pl. World 2:4–7. 1878) describing the same hybrid less technically, and because Davenport's combination in *Nephrodium* is a provisional and illegitimate name, the works cannot serve as the basis (protologue) for Hahne's epithet. Wherry (Bartonia 21:15. 1942) did not cite Davenport's paper, and probably he did not see Hahne's paper in accepting his epithet, for he did not publish any description. Nor did his later citation (Fern Guide. 128: 1961) of the hybrid formula *Aspidium cristatum* × *marginale* Davenp. in synonymy under *D. ×slossonae* validate the name because a hybrid formula is not equivalent to a species epithet, and so a description accompanying a hybrid formula is not a valid protologue. Therefore, the name *Dryopteris ×slossoniae* has until now not been validly published, for it has lacked a description. Lastly, the correct spelling of the epithet is *slossoniae;* the *−ii* following the consonant *n* must be altered to *−iae* because of Slosson's gender, in conformity with the International Code of Botanical Nomenclature.

Lycopodium ×brucei (Cranfill) Lellinger, comb. nov.

Lycopodiella ×brucei Cranfill, Amer. Fern J. 71:97. 1981. TYPE: Borrow pit ca. 200 m ENE of road KY-280 0.6 mi from its junction with road KY-121, Calloway County, Kentucky, *Bruce 76006* (MICH not seen).

This is the hybrid between *L. appressum* (Chapm.) Lloyd & Underw. and *L. prostratum* Harper.

I wish to thank Drs. J. D. Montgomery, D. H. Nicolson, and A. R. Smith for their helpful comments.—*David B. Lellinger, Dept. of Botany, National Museum of Natural History NHB-166, Smithsonian Institution, Washington, DC 20560.*

GRAVES' SPLEENWORT IN OHIO.—*Asplenium ×gravesii* Maxon is the apparent hybrid between *A. bradleyi* D. C. Eaton and *A. pinnatifidum* Nutt. Graves' Spleenwort has been reported only from Alabama, Arkansas, Georgia, Illinois, Missouri, Tennessee, and West Virginia (Cranfill, "Ferns and Fern Allies of Kentucky," p. 164–166, 1980; Wagner, Evolution 8:103–118. 1954; Wagner & Darling, Brittania 9:57–63. 1957; Werth & Taylor, Amer. Fern J. 70:28. 1980). Among these sources, Ohio also is included in the distribution of Graves' Spleenwort by Cranfill and Wagner. A search of herbaria housing large collections of Ohio pteridophytes has failed to locate a specimen confirming these reports. Moreover, the important description of this hybrid by Wagner & Darling (1957) does not list this taxon from Ohio. This is now a moot point, however, since a population of Graves' Spleenwort is extant in the state.

Three plants of *Asplenium ×gravesii* were discovered on 22 February 1983 in Hocking County, Ohio (*Cusick 22355*, MICH, OS). The site was revisited on 15 February 1984 in the hope of locating additional specimens, but no others were found. The hybrid grows on a sunny, southeast-facing exposure of the Black Hand Sandstone, a massive subacid sandstone of Mississippian age. The xeric, nearly vertical cliff also supports an extensive population of *Asplenium ×trudellii* Wherry, with scattered individuals of *A. pinnatifidum*. No plants of *A. bradleyi* were discovered, despite a careful search of this exposure and of other rock faces in the immediate vicinity. Indeed, Bradley's Spleenwort has been collected only once in this part of Ohio. A single population of *A. bradleyi* grew on a similar cliff in adjacent Fairfield County until at least 1971. It is no longer known from that site, however. Three other spleenworts grow on rock exposures within 2 km of the *A. ×gravesii* population. These are: *A. montanum* Willd., *A. platyneuron* (L.) B.S.P., and *A. trichomanes* L. The first two species are widely scattered through the whole valley system, while the Maidenhair Spleenwort is decidedly uncommon.

I thank Dr. Charles Werth, University of Virginia, for sharing with me his thoughts on spleenwort hybrids and Daniel Rice, ODNR, for field assistance. —*Allison W. Cusick, Division of Natural Areas & Preserves, Ohio Department of Natural Resources, Fountain Square, Columbus, OH 43224.*

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The Habitat Characteristics and Abundance of Equisetum ×ferrissii and its Parent Species, Equisetum hyemale and Equisetum laevigatum, in Iowa

LORENZ M. RUTZ and DONALD R. FARRAR*

Equisetum ×*ferrissii* Clute is the naturally occurring sterile hybrid of *E. laevigatum* A. Br. and *E. hyemale* var. *affine* (Engelm.) A.A. Eaton (Hauke, 1958). Although it is morphologically distinct and relatively easy to identify, it does not consistently appear on floristic lists of Iowa's prairies, nor in broader discussions of Iowa or Midwest floras. Only recently has the commonness of *E.* ×*ferrissii* become recognized. Peck (1976) documented the presence of *E.* ×*ferrissii* in 74 of Iowa's 99 counties. He felt (pers. comm.) that a thorough search would turn up *E.* ×*ferrissii* in the remaining counties as well, making it as widespread in Iowa as its parent species. *E. hyemale* has been recorded in all counties, and *E. laevigatum* in 91 of 99 counties. The current study was designed to quantify the presence of *E.* ×*ferrissii* in one county considered representative of much of Iowa and to address ecological questions regarding the dispersal and maintenance of the sterile hybrid and its parental species.

Ecological information on these three *Equisetum* taxa is sparse. Hartman (1958) recognized what are now known as *E.* ×*ferrissii* and *E. laevigatum* as plants of ditches and embankments, noting also that *E.* ×*ferrissii* grew in moister sites than *E. laevigatum* and that *E. hyemale* preferred a moister habitat than either *E.* ×*ferrissii* or *E. laevigatum*.

Because they are agricultural weeds and toxic to livestock, *E. palustre* and *E. arvense* have received considerable attention. Borg (1971) did an extensive study on *E. palustre* as a weed in Finland. He recorded rhizome growth of 30 cm to several meters per year, reaching depths of 180 cm below the soil surface. In regard to vegetative dispersal, he found that rhizome fragments of *E. palustre* were not good propagules and did not support the idea that *E. palustre* was spread by road building activity.

As field weeds, *E. palustre* and *E. arvense* have been tested for herbicide responses. *E. arvense* topgrowth was found to be sensitive to most chemicals, and rhizome growth could be retarded to various degrees (Hoyt & Corder, 1962). *Equisetum palustre*, on the other hand, was found to be quite resistant to the chemicals tested. Topgrowth could be damaged, but rhizomes remained virtually unaffected (Holly, 1953).

The ease of vegetative propagation in *Equisetum* has been noted several times (Hauke, 1963; Praeger, 1934; Schaffner, 1931; Wagner and Hammitt, 1970). The reports concentrate on the proliferation of aerial culm fragments floating on water or placed in or on saturated soil. Hauke (1963) suggested that *E.* ×*ferrissii* culms were transported outside the range of its parent species by human activity. He noted, however, that preventing desiccation during translocation was critical for success. Dosdall (1919) also found that culms rapidly lost viability upon drying and, in

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contrast to Borg's findings (1971), that rhizome fragments were the most suitable propagules for starting *Equisetum* in drained soil.

Sexual reproduction in *Equisetum* has been studied mostly in laboratory cultures, but Duckett and Duckett (1980) described the ecology of *in situ* gametophytes of *E. arvense*, *E. fluviatile*, and *E. palustre* in Great Britain. The sites described were previously flooded muds, bare of vegetation. They found that spores and gametophytes had a very low range of moisture tolerance and proposed this as an explanation for the frequent absence of gametophytes in apparently suitable sites.

Gametophytes in the American Midwest were discovered by Walker (1921, 1931) on stream banks in Iowa, Nebraska, and Kansas. All gametophytes were found on the narrow mudbelt along the water, typically associated with *Riccia*. Unfortunately, Walker's identifications must be treated with caution for two reasons. She reported gametyophytes of "*E. kansanum*" and *E. "laevigatum,"* which are now known respectively as *E. laevigatum* and the sterile (!) *E. ×ferrissii*, and, according to Walker (1931), the identifications depended "entirely upon the species growing in the vicinity."

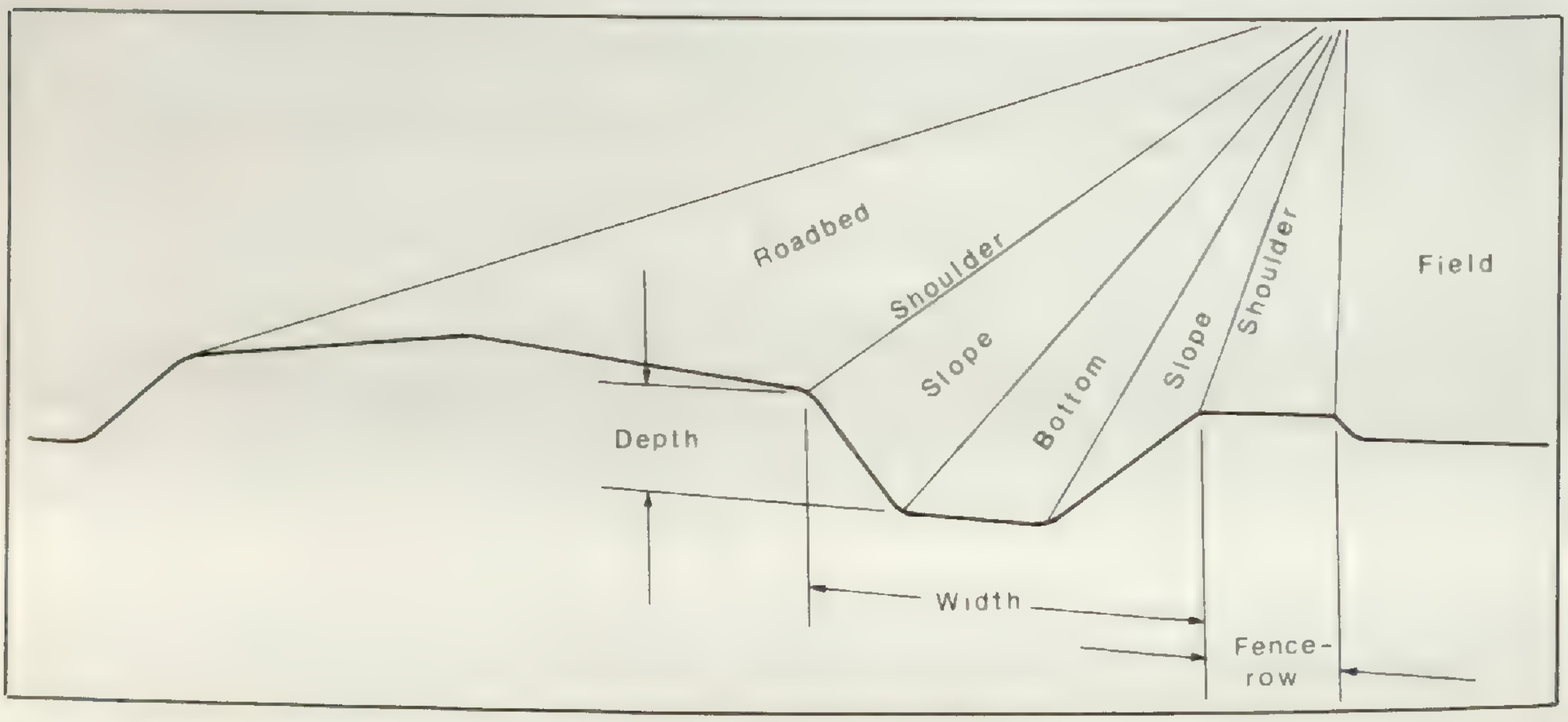

FIG. 1. Schematic cross section of a typical Iowa road showing ditch features; not drawn to scale.

METHODS

Natural areas in central and northwestern Iowa were visited to gain familiarity with the three taxa in their native habitats and in roadside ditches. Hauke's (1963) monograph was used to identify the plants.

To quantify the relative frequencies of the three taxa, and to obtain ecological information on ditch populations, a survey of 64 miles (103 km) of roadside in Story County, central Iowa, was made on foot in the summer of 1981. Story County is composed of 16 townships of 36 sections each. Sections are one mile (1.6 km) square and usually are delimited on four sides by roads. The roads are bordered on each side by ditches 4–10 m wide and 1–1.5 m deep, depending on the road type (*Fig. 1*). Information regarding the design, construction, and maintenance of Iowa's roads and ditches was obtained from the Iowa Department of Transportation (IDOT).

TABLE 1. PRESENCE OF *Equisetum* SUBGENUS *Hippochaete* IN IOWA PRESERVES OF NATIVE VEGETATION.

Preserve	*Vegetation type*	*Equisetum laevigatum*	*Equisetum ×ferrissii*	*Equisetum hyemale*
Bixby State Park Clayton Co.	Forest	–	–	+
Black's Prairie Story Co.	Prairie	+	+	–
Cayler Prairie Dickinson Co.	Prairie	+	+	–
Crossman Prairie Howard Co.	Prairie	+	–	–
Dolliver State Park Webster Co.	Forest	–	–	+
Doolittle Prairie Story Co.	Prairie	+	–	–
Freda Haffner Kettlehole Dickinson Co.	Prairie	+	+	–
Gitchie Manitou State Preserve Lyon Co.	Prairie & forest	+	+	+
Hayden Prairie Howard Co.	Prairie	+	+	*
Kalsow Prairie Pocahontas Co.	Prairie	+	–	*
Ledges State Park Boone Co.	Forest	–	–	+
Woodman Hollow State Preserve, Webster Co.	Forest	–	–	+

+ = present, – = not observed, * = present only as invasion from bordering roadside ditch

the Story County Engineer, and the Story County Weed Commissioner.

The survey unit was the four ditches bordering a section. If any of the four were missing, the equivalent ditch of the adjacent section was surveyed. One "primary" section in each of eight alternating townships was selected randomly. Along primary sections, the following ditch and *Equisetum* stand characeristics were measured: drainage, topographical position, ditch depth, apparent soil drift, species richness (number of species present), road type, ditch position relative to field (N, E, S, W), estimate of snow drift, *type and width of fencerow, *adjacent field use, *soil parent material, *slope of ditch bottom, kind of *Equisetum*, overall density of the stand, maximum density found in the stand, height of *Equisetum*, stand length, *stand width, *percent of culms with cones, and *health of plants. Asterisked characteristics were found to be closely linked to others or essentially non-varying. For clarity of presentation, these are not included in the results.

To obtain a larger statistical base for abundance data, two "secondary" sections were likewise selected from each of the eight townships. Along these sections, only the taxon present, stand length, and overall density were recorded. Data from secondary sections is included only in *Table 2*. *Equisetum* stands typically occupied the entire ditch from fence row to road bed. Thus stand length, measured parallel to the road, was directly proportional to the total physical extent of the stand.

TABLE 2. RELATIVE ABUNDANCE OF *Equisetum laevigatum*, *E.* ×*ferrissii*, and *E. hyemale* IN ROADSIDE DITCHES IN STORY COUNTY, IOWA.

Taxon	*Sections*	*No. of stands*	*Sum of stand length (m)*	*Average stand length (m)*	*No. of stands*[1]		
					Low density	*Medium density*	*High density*
E. laevigatum	Primary	166	22,370	135	80	59	53
	Secondary[2]	198	22,445	113	93	74	34
	Total	364	44,723	123	173	133	87
E. ×*ferrissii*	Primary	60	3,868	64	53	7	0
	Secondary[2]	50	2,923	59	40	10	1
	Total	110	6,791	62	93	17	1
E. hyemale	Primary	8	611	76	1	3	4
	Secondary[2]	9	1,363	152	2	1	6
	Total	17	1,974	116	3	4	10
All	Grand total	491	53,291	109	268	154	98

[1]Low = 0–50 culms per square meter, med = 50–200, high = 200–400. Some extensive stands were measured at several points along their length.

[2]Time constraints allowed the survey of only half of the secondary sections initially selected, consequently their distribution was biased towards the north portion of the county.

OBSERVATIONS AND RESULTS IN NATURAL HABITATS

Prior to European settlement, Iowa lands formed a network of upland prairies, prairie potholes, and prairie and woodland streams, providing an abundance of habitats suitable to *E.* ×*ferrissii* and its parent species. The distribution of the three taxa, as observed in natural areas of a number of Iowa's parks and preserves, reflects this earlier distribution *(Table 1)*.

Equisetum hyemale is common on the banks and terraces of Iowa's creeks and rivers. It may become a dominant part of the understory of the gallery forest, attaining densities, at Ledges State Park for example, of 500 culms per square meter over large areas. Stands continue along tributary branches to various degrees, sometimes well into steep gullies with only intermittently flowing water. Low density stands occasionally appear on old terraces well above the present floodplain. An example of this occurs at Woodman Hollow State Preserve. *Equisetum hyemale* grows on or very near the water table. Subsurface soils of this habitat are unlikely to ever become dry.

Stands of *E. laevigatum* and *E.* ×*ferrissii* in native Iowa habitats always occur in full sunlight on prairie uplands. In undisturbed prairie, both may occur conspicuously or in very low densities. The presence of *E. laevigatum* at Crossman Prairie was substantiated by only two individual culms. In disturbed areas of native prairies, densities become substantially higher. Along an old drainage ditch cut through the northwest corner of Kalsow Prairie, for example, *E. laevigatum* attains densities of 60 culms per square meter. *E.* ×*ferrissii* is less frequent than *E. laevigatum*, but it also is not uncommon in native prairie habitats.

Soils in Iowa's prairies range from dry to very wet, reflecting the poor drainage conditions of much of northern and central Iowa prior to artificial drainage by European settlers. As with soils of the native riparian habitat of *E. hyemale*, it is unlikely that the more poorly drained prairie soils ever become dry. *Equisetum laevigatum*, however, grows on higher, well-drained sites, along the rim of the Freda

Haffner Kettlehole in northwestern Iowa, for example. The substrate there is a coarse glacial till, which becomes very dry in summers of sparse rainfall. *E.* ×*ferrissii* grows in the same area, but is confined to the lower slopes of the kettle rim.

Two sites with *Equisetum* gametophytes were located. Sporophytes from these gametophytes were transplanted, allowed to mature in the greenhouse, and identified as *E. hyemale* in both cases. In the summers of 1980 and 1981, gametophytes of *E. hyemale* were common on the vertical cut bank of the Des Moines River at Ledges State Park. A few gametophytes were also found on the silts and muds of the level floodplain a few meters back from the bank. The second site was along the cut banks of Kegley's Creek in Story County (section 36, Lafayette Township). The cut banks at both sites were 1 –2 m high, kept moist by constant seepage, faced north to west, and received only late afternoon sun, if any at all. New sporophytes were common in late summer, but their fate was uncertain, as frost wedging cleaves most of the bank faces, burying the sporelings in mud. Associated plants included *Ricciocarpus natans* and *Riccia frostii*, several unidentified mosses, and a variety of angiosperm seedlings and annuals.

OBSERVATIONS AND RESULTS IN ROADSIDE DITCHES

As the prairies were converted to farmland, roads were cut into the landscape in the middle 1800's. *Equisetum* ×*ferrissii* and *E. laevigatum* were displaced from their native prairie but found a suitable habitat along the roadsides where they are now found in abundance. Today, with the virtual elimination of prairies, roadside ditches have become the primary habitat for *E.* ×*ferrissii* and *E. laevigatum*, and often provides suitable habitats for *E. hyemale* as well.

Characteristics of ditch stands of Equisetum.—The number, size, and distribution of stands among three density classes of each taxon was surveyed (*Table* 2). *Equisetum laevigatum* was by far the most common, having the largest number of stands and the greatest sum of stand length. Because of the difficulty in delimiting individual stands, the latter figure probably expresses the dominance of *E. laevigatum* more meaningfully than does the number of stands. The total length of ditch occupied by *E. laevigatum* was over six times that of *E.* ×*ferrissii*, which in turn was over three times that of *E. hyemale*. The total stand length of *E. laevigatum* alone represents 43% of the 103 kilometers surveyed. Discounting overlaps in stands, 52% of the extent of central Iowa's roadside ditches contains one of these three *Equisetum* taxa.

The distribution of stands in three density categories is different for each of the taxa (*Table 2*). *Equisetum laevigatum* stands regularly occur in all categories, but are more frequently of low or medium density. *Equisetum* ×*ferrissii* occurs almost exclusively as low density stands. *Equisetum hyemale* shows the opposite, occurring mostly as high density stands. This relationship is repeated in the mean densities shown in *Table 3*. The maximum density also indicated that *E.* ×*ferrissii* (21 culms m^{-2}) had by far the lowest density of the three taxa. *Equisteum hyemale* had the highest mean maximum density (156 culms m^{-2}), but did not greatly exceed *E. laevigatum* (105 culms m^{-2}).

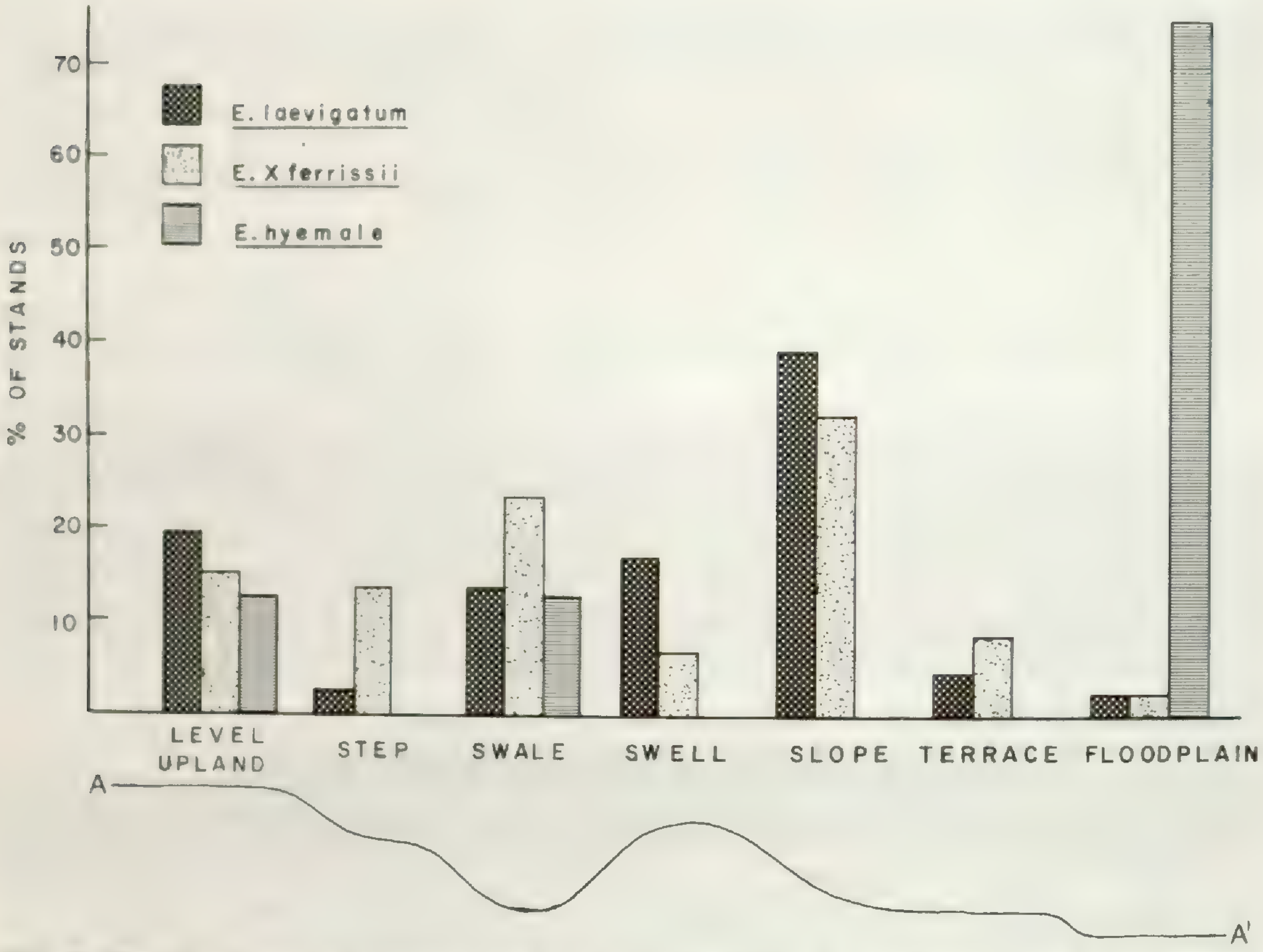

FIG. 2. The distribution of roadside stands of *E. laevigatum*, *E.* ×*ferrissii*, and *E. hyemale* by topographical position. Values are the percent of the total number of stands for each taxon. A—A′ = topographical cross section illustrating the categories listed.

The mean species richness (*Table 3*) in the ditches fell near nine for stands of all three taxa, a low, but expected value for such an impacted environment. Species richness ranged from 1 to 24 species, in addition to the *Equisetum* present. At several locations the single species growing with *E. laevigatum* was *Bromus inermis*.

The mean index values for road type, ditch depth, drainage, and soil drift (*Table 3*) indicate that *E. hyemale* occurred more frequently in deep ditches along paved roads than did *E. laevigatum* and *E.* ×*ferrissii;* the latter tended to occur in shallower ditches along gravel roads. Deeper ditches correspond with greater soil and snow accumulation and poorer drainage.

The topography of Story County was classified into the seven categories diagrammed in *Figure 2*, and the distribution of stands among these categories recorded. *Equisetum laevigatum* had a higher proportion of its stands in well drained areas (slopes and swells) than did *E.* ×*ferrissii*. In less well drained areas (steps, swales, and terraces), *E.* ×*ferrissii* had a higher proportion than *E. laevigatum*. Both were infrequent on the floodplains where *E. hyemale* had the greatest proportion of its stands. All three taxa occurred on the level upland.

The topographical preferences of *Equisetum* are repeated in the position of the maximum stand densities within ditches (*Table 4*). *Equisetum hyemale* grows most densely in the bottom of the ditch more often than does *E. laevigatum* or *E.*

TABLE 3. SELECTED MEANS FOR VARIABLES ON STANDS OF *Equisetum* IN PRIMARY SECTIONS, WITH STANDARD ERROR FOR CONTINUOUS VARIABLES IN PARENTHESES.

Variable	*E. laevigatum*	*E. ×ferrissii*	*E. hyemale*
No. of stands	166	60	8
Max. density (culms per m^2)	105(7.8)	21(3.6)	156(52)
Overall density[1]	1.8	1.1	2.3
Height (cm.)	70(1.5)	66(2.7)	92(9.1)
Diversity[2]	8.6(0.37)	8.5(0.60)	9.1(1.01)
Road type[3]	2.1	2.1	2.4
Ditch depth (ft.)	2.7(0.09)	2.5(0.13)	4.1(0.65)
Drainage[4]	2.2	1.9	1.2
Soil drift[5]	1.9	2.0	2.9
Snow drift[6]	1.5	1.6	1.9

[1] 1 = low (0–50 culms/m^2), 2 = med (50–200), 3 = high (200–400)
[2] number of other species present
[3] 1 = dirt road, 2 = gravel road, 3 = paved road
[4] 1 = poor, 2 = fair, 3 = good
[5] 1 = none, 2 = light, 3 = medium, 4 = heavy
[6] 1 = light, 2 = medium, 3 = heavy

TABLE 4. POSITION OF MAXIMUM DENSITY IN THE DITCH PROFILE AS DIAGRAMMED IN FIGURE 1[1]

	Aspect of ditch slope					
	N	S	E	W	*Shoulder*	*Bottom*
E. laevigatum	7%	31%	19%	18%	16%	9%
E. ×ferrissii	15%	26%	22%	7%	21%	9%
E. hyemale	9%	9%	18%	18%	18%	27%

[1] Since maximum densities sometimes occurred in more than one position in a single stand, the total number of scored positions is somewhat greater than the total number of stands.

×ferrissii, the latter preferring the slopes and shoulders. *Equisetum laevigatum* shows this effect most strikingly, often growing hedgelike, tallest and densest, on the ditch shoulders (*Fig. 5*). Of the slopes available, south-facing seems to be most preferred by *E. laevigatum* and *E. ×ferrissii*.

Characteristics of the ditch habitat.—To ecologically evaluate the roadside habitat of *Equisetum* in Iowa, it is necessary to consider the activities and conditions imposed upon plants in this habitat. The factors influencing the distribution and abundance of *Equisetum* in the ditch can be considered in two groups: human activities of construction, maintenance, and vegetation management, and inherent ditch characteristics, including the incidental effects of human activity.

The roads in Iowa can be classified into four categories: (1) interstate and other limited access highways, (2) paved state and county highways, (3) gravel section roads, and (4) dirt roads. Limited access highways contain many *Equisetum* stands, but these were not studied for legal and safety reasons. Dirt roads are few. They are minimally graded, lack the deep ditches characteristic of the other roads, and may be bordered directly by row crops or vegetation similar to that in the ditches. Dirt roads were included in the survey as they appeared in the selected sections.

By far the most numerous roads are the paved state and county roads and the gravel section roads. The most important feature of these two groups is the conspicuous ditch on either side of the roadbed (*Figs. 1, 3–5*). On new construction

FIG. 3. Winter ditch in Story County, Iowa, showing snow drift deposited by northerly winds. FIG. 4. Newly excavated ditch in Story County, Iowa. Vegetation in distance is still intact. FIG. 5. June ditch vegetation, showing strong growth of *E. laevigatum* along road edge.

and reconstruction projects, these are cut to an average depth of five feet (1.5m) for paved roads and three feet (0.9 m) for gravel roads. The ditches have two functions: water drainage and capture of drifting snow in winter to maintain a clear road with minimal plowing (*Fig. 3*). With time, the ditches become partially filled with soil and gravel, necessitating reconstruction.

Since there are few abrupt topographic changes in central Iowa, relatively little earth is moved in preparing new roadbeds. Most earth moving involves onsite relocation of ditch soil to the roadbed. However, in reconstruction, soil is often relocated considerable distances from shallow ditches to low areas on the roadbed. In one case which we observed, soil was transported over three kilometers. The excavated ditch, in this case, showed broken ends of *Equisetum* rhizomes, indicating that rhizome material was being relocated. These activities virtually eliminate other existing ditch vegetation (*Fig. 4*), but seem to have no long-term negative effects on *Equisetum* because the rhizomes generally extended deeper than the excavation. The remaining *Equisetum* rhizomes quickly resume growth in an environment with little competition from other species.

Another maintenance activity involves gravel roads only. About once per week during the summer, gravel roads are graded to smooth their surface. Two passes are made, moving gravel and chance roadside vegetation first to the road center, then across to the opposite shoulder. Inspection of debris moved in this operation frequently revealed *Equisetum* rhizomes.

Story County began a blanket 2,4-D spraying program shortly after World War II. The program lasted 25 years, ending in 1973. As a result, populations of dicotyledonous plants were reduced in size, if not eliminated. Only spot spraying is now practiced by the county; consequently, native and introduced dicotyledonous flowering plants are again becoming more common. Private spraying occurs along the field side of some ditches where farmers attempt to control weeds. The *Equisetum* taxa in this study occasionally showed herbicide damage. but were not eliminated by any of the commonly used chemicals. This herbicide resistance was emphatically attested to by farmers, extension personnel, and by the County Weed Commissioner.

The IDOT reseeds new or reworked roadsides with *Bromus inermis* (Smooth Brome), *Festuca arundinacea* (Kentucky 31 Fescue), *Coronilla varia* (Crown-vetch), and *Lotus corniculata* (Birdsfoot trefoil). County seeding is the same, with the addition of some prairie grasses, i.e. *Andropogon gerardii* (Big Bluestem) *Panicum virgatum* (Switch Grass), and *Sorghastrum nutans* (Indian Grass). Additional prairie species have been used in experimental plantings (Landers, 1968, 1970), but these have not been incorporated into the general management program for roadside vegetation.

The ditches are mowed by state and county governments and property owners. Official mowing is limited to one sickle bar's width along the road edge. Private mowing is not prohibited, however, and these practices range from manicured lawn to short, isolated cuts with sickle bar once to several times in mid- to late summer. *Equisetum* does not regenerate with sufficient rapidity to survive repeated close mowing. The effects of sickle bar cutting depend on the timing, frequency, and thoroughness of the cuts. *Equisetum laevigatum* and *E.* ×*ferrissii* put up a single flush of culms in late spring. Early cuts can be quite damaging, but the later the cut, the less damage to the stand. After a first flush, *E. hyemale* adds new culms all summer. It can recover from individual cuts, but a high frequency of cuts is more damaging to that species. Most ditches escape mowing entirely, either by choice of the landowner, or because they are too deep and narrow for mowing machinery.

A few landowners burn their ditches regularly. *Equisetum laevigatum*, in a ditch burned annually, was exceptionally healthy, uniform, and quite attractive.

Where roads cut through the rolling topography of Iowa, their ditches become areas of less extreme moisture conditions. In low, wet areas, the ditch locally depresses the water table and is artificially drained, making it a drying factor. On high, dry areas, the ditch is more moist than surrounding land, being closer to the water table and serving as a sink for seepage and runoff. In both situations, the ditch generally provides a drained but consistently moist habitat.

The ditches are bordered on both sides by extensive areas of unused or underused soil resources. The roadbed may be built of rich topsoil removed from the ditches. Adjoining fields (in 90% of the surveyed *Equisetum* stands) are fertilized and cultivated to within a meter or less of the ditch shoulder. On the other hand, soil in the ditch bottom is usually poor, being only slightly altered glacial till. It generally is dense and calcareous, and has little organic material.

The ditch serves as a sink for various materials. Chemicals leach from fields in the form of nutrients as well as toxic herbicides and pesticides. Automotive wastes

and trash drift in from the roadside. Large quantities of road gravel and topsoil accumulate, the latter delivered by winter winds and spring and summer runoff. When adjacent to fields without mulch or standing crops, dormant vegetation may be covered by several centimeters of powdered topsoil. Drifting snows accumulating in the ditches (*Fig. 3*) provide winter protection for ditch plants and augment spring moisture.

DISCUSSION

Equisetum ×*ferrissii* and *E. laevigatum* were inhabitants of the once extensive Iowa prairies. The principal habitat of these taxa in Iowa at present is the continuous system of roadside ditches. *Equisetum laevigatum* is by far the most frequent, occurring to some extent in each mile of road surveyed. *E.* ×*ferrissii* stands are usually much smaller, but their number is almost one third as great as that of *E. laevigatum*. *Equisetum hyemale*, a natural component of the gallery forests along Iowa's streams, has also successfully colonized these roadsides. It is the least frequent of the three taxa in this habitat, but thrives where it is established.

The current high frequency of *E. laevigatum* and *E.* ×*ferrissii* probably reflects their broad distribution before European settlement. The occurrence of *E. laevigatum* in all eight prairie preserves explored by the authors suggests that it was a ubiquitous component of the prairies that once covered most of the state. *Equisetum* ×*ferrissii*, though not so frequent in the prairies as *E. laevigatum*, is present in over half of the prairies surveyed and may also be assumed to have been quite common. As the land was surveyed and roads were cut in the middle 1800's, *E. laevigatum* and *E.* ×*ferrissii* probably lingered to some extent, more or less in place, and adopted the road borders as suitable habitats. Their current abundance cannot, however, be entirely explained through their historical occurrences. Few new roads are being built in Iowa today, but old ones are continually being maintained with attendant disturbance to ditch vegetation. Both taxa are present along newly constructed interstate and state highways. Furthermore, *E. hyemale* is not a natural component of the prairies; its presence in the ditches is due to colonization from some distance. Therefore, an explanation of the relative abundance of the three *Equisetum* taxa in the ditches must also include current patterns of reproduction and dispersal.

If one accepts Walker's (1921, 1931) identification of wild *E. laevigatum* gametophytes, they occur in the same habitat as those of *E. hyemale* described herein. Assuming temporal concurrence, this habitat concurrence makes the sexual formation of *E.* ×*ferrissii*, although undocumented in nature, regularly possible, and its abundance in pre-settlement vegetation understandable.

Although possible, it is unlikely that existing ditches can provide the combination of conditions necessary for the sexual formation of *E.* ×*ferrissii*, considering the narrow habitat tolerance of gametophytes (Duckett & Duckett, 1981). Although excellent habitat for mature sporophytes, modern ditches are too exposed, too well drained, and vegetatively too dense to provide suitable gametophyte habitats. It is conceivable that in early days of road construction in Iowa, the ditches were subject to greater erosion and greater moisture seepage, since the land was not yet artificially drained. Such ditches would have been more similar to stream banks, and perhaps suitable for gametophytes of *E. laevigatum* and *E. hyemale*.

Although Duckett and Duckett (1981) feel that sexual reproduction must occur for *Equisetum* dispersal, we feel that for the ditch habitat and the three taxa in this study it is not essential. Their presence and abundance in the ditches can be attributed to vegetative dispersal and persistence alone. Growth of rhizomes is rapid and can account for clonal expansion over large areas of continuously suitable habitat. If Borg's (1971) conclusions regarding the clonal spread of *E. palustre* are applied to these three taxa, it is also possible that their rhizomes could traverse the 30 feet (9.1 km) of roadbed between ditches. A more likely mechanism for crossing gravel roads is transport by grading.

Expansion of clones cannot account for the many disjunct populations found in the ditch habitat; some form of dispersal must occur. Aerial stem fragments of *Equisetum* have excellent propagative properties (Hauke, 1963; Praeger, 1934; Schaffner, 1931; Wagner & Hammitt, 1970), but their lack of resistance to desiccation and the general lack of continuous standing or moving water in the ditches make it improbable that culm proliferation accomplishes dispersal in ditches. Rhizome fragments transported in soil are far more likely propagules. Although apparently not the case for *E. palustre* (Borg, 1971), rhizome fragments of *E. hyemale*, *E. laevigatum*, and *E. ×ferrissii* maintain their viability if kept moist, and under such conditions even small fragments sprout readily (Rutz, 1982).

Earth-moving activities involved in road construction and maintenance also move *Equisetum* rhizomes and provide a very effective dispersal mechanism for these three taxa. Rhizomes are transported to adequately moist sites bare of competing vegetation. Once established, plants of *Equisetum* rapidly produce extensive rhizome systems (Borg, 1971; Rutz, 1982; Weaver & Albertson, 1943). Standard earth-moving practices are unlikely to eradicate deep rhizomes from a ditch site once they have become established.

Ditch habitats provide conditions both beneficial and detrimental to plant growth. Ditch moisture conditions are ideal for *Equisetum*, being drained but continually moistened by seepage and runoff. In the adjacent fields and on roadbeds, nutrients and moisture are available to plants able to exploit them. That the extensive rhizome system enables *Equisetum* to do this is evidenced by the appearance of culms up to 10 meters into cultivated fields, from the observation that *Equisetum* is a nuisance in plugging drainage tiles, and from the frequently observed increase in stand height and density along the road edge *(Fig. 5)*.

Detrimental characteristics of the ditches include the high level of herbicides and other chemicals and the constant additions of soil and gravel. However, *E. hyemale*, *E. laevigatum*, and *E. ×ferrissii*, like *E. palustre* (Holly, 1953), appear to be largely immune to herbicide damage and possibly benefit through reduced competition from dicotyledonous plants. Likewise, soil sedimentation presents no problem to the rhizomatous *Equisetum*.

Perhaps the only aspect of the ditch habitat truly detrimental to *Equisetum* is mowing. None of the three *Equisetum* taxa can survive repeated close mowing, but this condition is rare. The degree to which they are affected by maintenance mowing depends on frequency and timing of the cuts. Generally mowing aims to eliminate dicotyledonous weeds and is not of sufficient frequency to damage *Equisetum*.

Although artificial, the continuous network of Iowa's roadside ditches is a significant habitat, serving as a refuge for many native species. The common occurrence of all three *Equisetum* taxa in the roadside habitat and the suitability of this habitat to quantitative survey techniques and experimentation provide an excellent opportunity for the ecological comparison of the three taxa. We feel that results based on roadside ditch observations and experiments provide relevant insight into the ecology of *Equisetum* in native habitats, as well as providing an explanation for the remarkable success of the sterile hybrid *E.* ×*ferrissii* and its parent species in Iowa's roadside vegetation habitats.

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The Organic Nutrition of Botrychium Gametophytes

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In studies on the green, thalloid gametophytes of leptosporangiate ferns, sugars have been added to the nutrient media to promote gametophyte growth. The commonly used sugar has been sucrose (Dyer, 1979). In comparative studies with several sugars, sucrose and glucose have given the best growth (Hurel-Py, 1955; Whittier, 1964). Other sugars which have supported the growth of some gametophytes are fructose, maltose, ribose, and xylose (Hurel-Py, 1955; Courbet, 1957; Whittier, 1964). Other studies have shown how exogenous sugars can alter gametophyte development and morphology (Whittier & Steeves, 1960).

Very little is known about the organic nutrition of the white, fleshy gametophytes of the Ophioglossaceae, compared with the green, thalloid gametophytes of the leptosporangiate ferns. It is generally accepted that the mycorrhizal fungus supplies the organic nutrients required because young gametophytes from germinating spores fail to grow beyond a few cells unless infected by a mycorrhizal fungus (Campbell, 1911) and mature gametophytes from nature always contain an endophytic fungus. There have been a few reports of gametophytes of the Ophioglossaceae in nature turning green at the soil surface, but it is doubtful if these gametophytes were self-sufficient (Boullard, 1963). The few studies on *Ophioglossum* and *Botrychium* gametophytes in axenic culture have shown that the gametophytes will grow to maturity if the nutrient medium contains sucrose (Whittier, 1972; Gifford & Brandon, 1978; Whittier, 1983). Thus, the endophytic fungus is not required for gametophyte growth or normal morphology in axenic culture.

The seeds of orchids are similar to the gametophytes of the Ophioglossaceae because they require a mycorrhizal fungus in nature and grow on nutrient media supplemented with soluble sugars in axenic culture. Orchid seeds will not germinate on a medium containing insoluble carbohydrates in axenic culture. Arditti (1967) has noted that if orchid embryos did exhibit extracellular digestion, the role of the mycorrhizal fungus would have to be reexamined. It has never been determined if *Botrychium* gametophytes can metabolize insoluble organic materials in axenic culture or from the soil. Any possibility that these gametophytes can obtain all or some of their carbon from the soil should be investigated. Preliminary tests can be performed to determine if these gametophytes exhibit extracellular digestion with the techniques of axenic culture.

Since only sucrose has been used as a carbon source for the gametophytes of the Ophioglossaceae, additional studies are necessary to determine what other exogenous carbon sources, soluble or insoluble, will support gametophyte growth. More complete information about the organic nutrition of these gametophytes should provide methods for accelerating the growth of these slow growing organisms and give a better understanding of what the mycorrhizal fungus is supplying to the gametophytes.

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MATERIALS AND METHODS

This study was initiated with spores of *Botrychium dissectum f. obliquum* (Muhl.) Fern. collected in Nashville, Tennessee. Voucher specimens of plants from which the spores were collected are on deposit at the Vanderbilt University Herbarium (VDB). The experimental conditions were tested on both spores and gametophytes of *B. dissectum*. The spores were surface sterilized and sown on nutrient media by the methods of Whittier (1973). For the experiments which were initiated with gametophytes, the gametophytes were supplied from stock cultures maintained on the basic mineral medium with 0.5% sucrose in the dark.

The basic mineral medium was composed of Knudson's solution of mineral salts, FeEDTA, minor elements, 0.6% agar, and had a pH of 6.1 (Whittier, 1973). The cultures were grown on 15 ml of medium in 125×20 mm culture tubes with screw caps. The cultures were maintained in the dark at $24 \pm 1°C$. The duration of the experiments averaged 4 months for those initiated with spores and 3 months for those initiated with gametophytes.

The majority of the experiments involved supplementing the basic mineral medium with various potential carbon sources. The organic supplements and their concentrations are given with the results. There were several replicates for each treatment, and many experiments were repeated. The percentage of germination was obtained by observing 1000 spores from each experimental treatment. Thirty young gametophytes growing from spores and an average of 20 older gametophytes were measured to determine the gametophyte growth for each treatment. It should be noted that spores of *B. dissectum* will germinate and the young gametophytes will undergo a limited amount of growth on a nutrient medium without a carbon source.

Growth of the young gametophytes from spores is expressed as the percent increase in gametophyte length over spore diameter. In experiments with older gametophytes, growth is expressed as the percent increase in length over the initial gametophyte size. In the experiments which were initiated with measured older gametophytes, efforts were made to start with gametophytes of similar size. All measurements were made with a calibrated ocular micrometer.

In many experiments, especially those on the effect of substances other than sugars, a medium with 0.5% sucrose was included as a control to demonstrate that the spores were viable and that the older gametophytes, obtained from stock cultures, were alive and capable of growth. The growth of the gametophytes on the medium with 0.5% sucrose should only be used for comparative purposes within individual experiments. The percent increase in the lengths of both young and older gametophytes on 0.5% sucrose varied considerably among the experiments for two reasons. The durations of the experiments varied to some extent. Secondly, the initial size for the older gametophytes was not constant for all experiments. Thus, any increase in length would give a higher percent increase in length if smaller gametophytes were used instead of larger gametophytes to initiate an experiment.

The data on gametophyte growth are presented with the standard error of the mean. The analysis of variance and Duncan's multiple range test (Li, 1964) were used to determine if the differences among the means were statistically significant at the 1% confidence level. Within individual experiments, the means for the growth of

TABLE 1. THE EFFECT OF SURFACE STERILIZATION OF SPORES ON YOUNG GAMETOPHYTE GROWTH.

Surface sterilized	*% increase in gametophyte length*	*% germination*
Spore	880.7 ± 50.8a	6.1
Sporangium	905.7 ± 59.2a	4.8

TABLE 2. THE EFFECT OF LIGHT ON THE GROWTH OF OLDER GAMETOPHYTES.

Medium	*% increase in gametophyte length*	
	Light	*Dark*
Minerals only	4.4 ± 1.5a	2.1 ± 2.3a
Sucrose 0.25%	283.4 ± 22.4b	300.8 ± 38.6b

the young or old gametophytes followed by the same letter are not significantly different at the 1% confidence level.

These are the basic procedures and conditions used to determine effective carbon sources for spore germination and gametophyte growth with *Botrychium dissectum*. Any exceptions or modifications to these procedures, which had to be made in some experiments, are discussed with their related results.

RESULTS

In the past studies on *Botrychium* gametophytes in axenic culture, the spores were surface sterilized with 20% Clorox for 2 minutes. Because the spores germinated and the gametophytes grew, it was assumed that the Clorox treatment had no adverse effect. Because young gametophyte growth is used as a measure of the effectiveness of a carbon source, the effect of the Clorox treatment on germination and on young gametophyte development was examined. Sporangia were surface sterilized for 20 minutes with 25% Clorox. The spores from these sporangia were collected under axenic conditions and divided into two batches. Spores from the first batch were dusted on the nutrient medium. Spores from the second batch were surface sterilized with the usual 20% Clorox treatment, washed with sterile water, suspended in sterile water, and pipetted onto the nutrient medium. Between the two treatments, there was little difference in the percentage of germination and the difference in the growth of young gametophytes was not statistically significant (*Table 1*). In addition, other experiments have shown that spores of *Botrychium dissectum* can be treated up to 8 minutes with 20% Clorox before germination is inhibited.

Since light inhibits the germination of *Botrychium* spores (Whittier, 1973), a preliminary experiment was carried out to determine if light affected the growth of older gametophytes. Gametophytes were cultured in the light (12 hours of light per day; intensity 1400 lux) on media with or without a carbon source (*Table 2*). Light did not promote gametophyte growth on the basic mineral medium. Light also had no effect on gametophyte growth with sucrose present. Thus, exposing older gametophytes to light for transferring and measuring will not alter gametophyte growth. Since growing the gametophytes in the dark better simulated natural conditions, all gametophytes were grown in the dark for the remaining experiments.

TABLE 3. THE EFFECT OF SOIL ON GAMETOPHYTE GROWTH.

Treatment	*% increase in gametophyte length*	
	Old	*Young*
Soil A	1.7 ± 1.6a	79.3 ± 4.6a
Soil B	−0.2 ± 1.3a	———
Minerals only	1.2 ± 1.4a	82.5 ± 3.6a
Sucrose 0.5%	69.8 ± 23.0b	1051.6 ± 57.8b

TABLE 4. THE EFFECT OF VARIOUS SUCROSE CONCENTRATIONS ON GAMETOPHYTE GROWTH.

Percent sucrose	*% increase in gametophyte length*		*% germination*
	Old	*Young*	
0.25	56.1 ± 9.7d	180.7 ± 18.1b	9.7
0.5	101.9 ± 11.8cd	262.0 ± 30.8ab	9.2
1.0	176.2 ± 18.3c	276.0 ± 23.4a	9.8
2.0	470.4 ± 54.9b	283.6 ± 18.6a	9.3
4.0	587.9 ± 35.9a	206.0 ± 16.5ab	8.7

Campbell (1911) observed that soil would not support the growth of young *Ophioglossum* gametophytes. He found that without the interaction of a mycorrhizal fungus, the germinating spores produced gametophytes of only 3 or 4 cells. To test these observations, spores were sown on autoclaved soil from a site in Tennessee where *Botrychium* gametophytes had been collected (*Table 3*). The percentage of germination is not reported because it was impossible to recover large numbers of spores from the soil cultures. The growth of young gametophytes on the soil was similar to the minimal growth of gametophytes which occurred on the basic mineral medium. The young gametophytes on the soil and on the mineral medium stopped growing at the 4- or 5- celled stage. The older gametophytes were taken from the stock cultures and placed on the basic mineral medium or on autoclaved soil from two sites in Tennessee where gametophytes had been found. No gametophyte growth occurred on the soil cultures or on the mineral medium after 2.5 months. The gametophytes from the stock cultures were healthy and capable of growth because those placed on the medium with 0.5% sucrose did grow (*Table 2*).

The carbon source for the previous studies on gametophytes of the Ophioglossaceae in axenic culture has been sucrose (Whittier, 1972, 1983; Gifford & Brandon, 1978). In these studies, the sucrose had been autoclaved in the basic mineral medium. Minor changes do occur to sucrose during autoclaving (Ball, 1953). Spores were sown on a medium with filter-sterilized sucrose (0.5%) to determine if gametophyte growth was improved over that on a medium with autoclaved sucrose (0.5%). There was no significant difference in the percent increase in length of young gametophytes on filtered sucrose (304 ± 18.6) and autoclaved sucrose (322 ± 19.8). For the remaining experiments, the sucrose and other organic components of the media were not filter sterilized.

Experiments to determine the optimal concentration of sucrose for gametophyte growth were carried out with sucrose concentrations of 0.25–4.0% (*Table 4*). There was little variation in the percentage of germination on the various sucrose concen-

TABLE 5. THE EFFECT OF VARIOUS SUGARS AT 0.5% CONCENTRATION ON GAMETOPHYTE GROWTH.

Treatment	*% increase in gametophyte length*		*% germination*
	Old	*Young*	
Sucrose	365.1 ± 32.3ab	372.0 ± 34.4b	4.5
Glucose	431.5 ± 31.9a	416.6 ± 44.8ab	4.8
Mannose	438.7 ± 42.9a	425.4 ± 50.2a	4.7
Trehalose	223.3 ± 25.1cd	408.4 ± 48.7ab	4.8
Fructose	306.9 ± 19.3bc	250.7 ± 8.7c	4.6
Cellobiose	111.2 ± 14.2de	209.0 ± 15.2cd	4.7
Maltose	75.1 ± 16.2e	180.2 ± 12.7d	4.4
Minerals only	0.7 ± 1.8e	76.3 ± 2.3e	4.2

trations. The older gametophytes grew best on 4% sucrose. However, the difference in growth on 4% and 2% sucrose was less than the difference between the 2% and 1% sucrose concentrations. It would appear that the growth of these gametophytes was beginning to level off at 4% sucrose. The younger gametophytes grew best at 2% sucrose. However, the differences in the amount of growth on the 0.5–4.0% concentrations of sucrose were not statistically significant. Less growth occurred on the medium with 4% sucrose than at 2% sucrose, which may have been due to the osmotic concentrations of the medium with 4% sucrose.

Because the higher concentrations of sucrose inhibited the growth of young gametophytes, all other sugars were tested at a 0.5% concentration. Preliminary tests showed that the pentoses, xylose and ribose; the hexoses, galactose, sorbose, and rhamnose; the disaccharides, lactose and melibiose; and the trisaccharide, raffinose, did not support the growth of young gametophytes. Further testing was completed on six sugars, in addition to sucrose, which had supported the growth of young gametophytes in the preliminary tests (*Table 5*). The best growth for both the young and older gametophytes was obtained with the hexoses, glucose and mannose. However, the difference in the growth by the older gametophytes on glucose, mannose, and sucrose was not statistically significant. With young gametophytes, trehalose gave almost the same growth as glucose and mannose. In both young and older gametophytes, the poorest sugars for supporting growth were the disaccharides, maltose and cellobiose. Spore germination was essentially the same for the various sugars.

In symbiotic associations between fungi and other plants, sugar alcohols may be produced by either of the symbionts and may move between the symbionts (Lewis & Harley, 1965; Smith, 1967; Hill & Smith, 1972). Also, some fungi are known to accumulate mannitol in their mycelium (Turner, 1971). Consequently, three common sugar alcohols were tested on *Botrychium* gametophytes. Mannitol, inositol, and sorbitol at concentrations of 1% had no effect on germination and did not support the growth of young or older gametophytes.

Although the gametophytes appear to require a mycorrhizal fungus for growth in the soil, the possibility that *Botrychium* gametophytes might be able to break down insoluble organic materials in the soil for growth has not been adequately tested. The soils used in the earlier experiments *(Table 3)* may not have contained enough

TABLE 6. THE EFFECT OF INSOLUBLE CARBOHYDRATES ON GAMETOPHYTE GROWTH.

Treatment	*% increase in gametophyte length*		*% germination*
	Old	*Young*	
Starch 2.0%	0.4 ± 2.6a	67.4 ± 3.1a	4.4
Cellulose 2.0%	0.6 ± 2.2a	61.1 ± 2.8a	4.2
Sucrose 0.5%	60.4 ± 6.5b	372.0 ± 34.4b	4.5
Minerals only	0.8 ± 1.5a	68.1 ± 2.5a	4.2

TABLE 7. THE EFFECT OF GLYCERINE ON YOUNG GAMETOPHYTE GROWTH.

Treatment	*% increase in gametophyte length*	*% germination*
Glycerine 0.5%	266.0 ± 20.8a	9.6
Sucrose 0.5%	339.2 ± 30.2a	9.0
Minerals only	67.4 ± 3.1	9.5

humus or organic matter to support gametophyte growth. The use of insoluble organic materials in the soil by the gametophytes depends on their ability to carry out extracellular digestion. Therefore, it was of interest to determine if *Botrychium* gametophytes could metabolize insoluble carbon sources in the external medium.

Several insoluble carbon sources were incorporated into the nutrient medium to determine if gametophytes could utilize exogenous, insoluble organic materials. In preliminary experiments, dextrin did not support the growth of older gametophytes. Starch (2%) and cellulose (2%) had no effect on germination and did not support the growth of young or old gametophytes *(Table 6)*. Treating the nutrient medium with I_2KI demonstrated that there was no starch breakdown in the medium adjacent to the older gametophytes. Spores also were sown in petri plates on emulsified nutrient media containing triglycerides. Young gametophytes on media with emulsified trihexonin, tristearin, and tripalmatin did not exceed gametophyte growth on the basic mineral medium. Germination was unaffected by the triglycerides.

Of the carbon sources tested on these gametophytes to this point, only the soluble sugars promoted gametophyte growth. However, sugars are not the only organic materials which will support the growth of *Botrychium* gametophytes. Spores sown on a medium supplemented with glycerine *(Table 7)* germinated and the gametophytes grew. Although the growth with glycerine was somewhat less than that on the same concentration of sucrose, the difference was not statistically significant. The effect of glycerine on the growth of older gametophytes was not examined.

As controls for many experiments, older gametophytes were placed on the basic mineral medium to show how much growth occurred after the gametophytes had been removed from the stock cultures which contained sucrose. The maximum change in length in the dark, the usual condition for these experiments, was a 2% increase after 4 months *(Table 2)*. These gametophytes taken from stock cultures contained starch, yet essentially no growth occurred. In addition to the gametophytes placed on the basic mineral medium, gametophytes placed on media containing starch and cellulose also exhibited no growth *(Table 6)*. The possibility that these older gametophytes cultured on the basic mineral medium or on a medium without a usable carbon source had died was tested. Gametophytes on a mineral medium

which increased in length 1% in two months, when transferred to a medium with 0.5% sucrose had an increase in length of 34% in one month. Gametophytes which had a minimal increase in length on media with 2% starch or 2% cellulose after 4 months *(Table 6)* increased in length 57% and 64% respectively in four months on 0.5% sucrose. Thus, they remained alive for as long as four months without a usable, exogenous carbon source and resumed growth when sucrose was available.

DISCUSSION AND CONCLUSIONS

Although the primary objective of this study has been to investigate the organic nutrition of *Botrychium* gametophytes, information about other questions on the biology of these gametophytes has been obtained.

Early observations (Campbell, 1911) that wet areas in the soil were the best places for the germination of *Ophioglossum* spores may not be true for all spores of the Ophioglossaceae. *Botrychium* spores obtained sterilely from sporangia and dusted directly on the solid nutrient medium germinated without difficulty. Liquid water is not necessary for the germination of *Botrychium dissectum* spores.

In most of the experiments, the percentage of spore germination was determined. There was some variation in the percentage of germination among the experiments. which would be expected since the duration of the experiments was not exactly the same. However, it should be noted that none of the treatments in this study stimulated (allowed) more than 10% of the spores to germinate. All the spores appear to have normal cytoplasmic components and are fully formed, thus it would seem that all the spores should germinate. If the spores are normal and viable, as they appear to be, then conditions for maximum germination have not been found with this study.

The carbohydrate nutrition of plant tissue and plants in axenic culture has been investigated over the years by determining which carbohydrates will support growth. Sugars are the usual carbon source for these cultures, although insoluble carbohydrates have been used occasionally (Street, 1969). The sugars that commonly support excellent growth are sucrose, fructose, and glucose for plant tissues (Street, 1969) and orchid seedlings (Withner, 1959). Similar results have been obtained with gametophytes of leptosporangiate ferns, although for some species fructose does not give the growth of glucose and sucrose (Hurel-Py, 1955). Since sucrose generally supports excellent growth or growth as good as other sugars, it is usually provided as the carbon source in attempts to grow new plants or plant tissues in axenic culture.

The few gametophytes of the Ophioglossaceae which have been grown in axenic culture were supplied with sucrose as the carbon source (Whittier, 1972, 1983; Gifford & Brandon, 1978). The concentration of sucrose in the medium can have important effects on the growth of *Botrychium* gametophytes. Increasing the concentration above 0.5% did not promote early gametophyte growth a significant amount. However, with older gametophytes the higher concentrations produced significant increases in gametophyte growth. The medium with 4% sucrose gave almost six times the growth as 0.5% sucrose. Thus, increasing the sucrose concentrations can accelerate the growth of older gametophytes and can produce mature gametophytes in short periods of time.

Of the other two sugars, glucose and fructose, which have been excellent carbon sources for many plant tissues, 0.5% glucose supported better growth of *Botrychium* gametophytes than 0.5% sucrose. Gametophytes grew on fructose, but to a lesser extent than on glucose or sucrose.

Trehalose was the only disaccharide, other than sucrose, to support good growth of these gametophytes. It was superior to sucrose as a carbon source for older gametophytes, but not for young gametophytes. Trehalose has not been commonly employed in other axenic cultures, but is known to support the growth of female gametophytes of *Selaginella* (Koller & Scheckler, 1982) and some orchid seedlings (Ernst, 1967).

An unusual aspect of the carbohydrate nutrition of *Botrychium* gametophytes was their use of mannose for growth. This was the only other sugar which supported growth of the gametophytes at a higher rate than sucrose. This is somewhat surprising because in other studies employing axenic culture techniques mannose is usually a poor carbon source (Street, 1969). With root and callus cultures, it ranges from being toxic, like galactose, to inert. Some gametophytes of leptosporangiate ferns can use mannose, but it supports a lower level of growth than do glucose or sucrose (Courbet, 1957; Whittier, 1964). However, for some orchid seedlings in axenic culture mannose is a better carbon source than sucrose (Wynd, 1933; Ernst, 1967).

With one or two minor exceptions, the use of soluble sugars by *Botrychium* gametophytes is comparable to that found in other plants or plant tissues in axenic culture (Street, 1969). Glucose and mannose supported better growth than sucrose for both older and younger gametophytes. It is possible that high concentrations of glucose and mannose will support more rapid growth and gametophyte maturation than higher concentrations of sucrose. Since at the lower concentrations the increase in growth on glucose or mannose over that on sucrose is relatively small, it is possible that higher concentrations of glucose or mannose may not give the hoped for increases in growth.

The only other substance which was found to support the growth of these gametophytes was glycerol. Thus, something besides a sugar will support gametophyte growth, although somewhat less than for sucrose at the same concentration. Although glycerol is not a common carbon source for plant tissues, it has been shown to support the growth of some callus tissues (Gautheret, 1948; Hildebrandt & Riker, 1955) and *Osmunda* gametophytes (Stephan, 1929).

The endophytic fungus has been considered the source of the organic materials for these gametophytes since Campbell (1911) reported that young *Ophioglossum* gametophytes did not grow beyond the three- or four-celled stage unless infected with a mycorrhizal fungus. This idea has been supported by the observations on older gametophytes from nature, which always contain a mycorrhizal fungus. Although it appeared doubtful, the possibility that the gametophytes obtain some or all of their organic materials from the soil was investigated. The gametophytes of *B. dissectum* did not grow on sterilized soil which had been obtained from areas having gametophytes. Thus, it would appear that the gametophytes cannot obtain enough organic nutrients from the soil to support growth.

Extracellular digestion would certainly be a requirement for these gametophytes to grow in the soil without a mycorrhizal fungus. Some plant tissues have demonstrated the ability to digest and use exogenous starch as a carbon source (Hildebrandt & Riker, 1953; Straus & LaRue, 1954). *Botrychium* gametophytes did not grow on media containing starch, cellulose, dextrin, or emulsified neutral lipids. In addition, no starch digestion occurred in the nutrient medium in contact with the gametophytes. There was no indication that *Botrychium* gametophytes have the ability to carry out extracellular digestion.

The organic nutrition of gametophytes of *Botrychium dissectum* in axenic culture is, with the exception of glycerol, dependent on the availability of soluble sugars. Although gametophyte growth remains relatively slow, increasing the sugar concentration, at least with sucrose, accelerates growth and maturation. With the appropriate concentrations of sucrose and possibly glucose or mannose, it would appear that the maturation time for gametophytes of *B. dissectum* can probably be reduced to about a year.

The theory that the mycorrhizal fungus supplies *Botrychium* gametophytes with organic materials necessary for growth has not been brought into question by any observations in this study. The gametophytes failed to grow on sterilized soil and on insoluble organic nutrients in axenic culture. These gametophytes did not carry out extracellular digestion. Thus, no evidence has been presented to alter the view that a symbiotic association with a mycorrhizal fungus is necessary for the organic nutrition of gametophytes of the Ophioglossaceae.

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REVIEW

A Taxonomic Revision of the Genus Grammitis . . . in New Guinea, by B. S. Parris. Blumea 29:13–222. 1983.—Of all the regions of the Old World tropics, New Guinea is the least known botanically. Copeland (Phil. J. Sci. 81:81–119, *t. 1–9*. 1953) published the only other account of the genus in New Guinea, and this contained only keys and a list of species with synonyms and distributions. Copeland included 48 species in *Grammitis sensu stricto*, whereas Parris has 64; the difference is due no doubt to the botanical explorations which have taken place since Copeland wrote. Parris' monograph is unusually complete. It contains both a dichotomous key and a multiple-entry key, as well as a conspectus of the species groups. A great many *Grammitis* species are endemic to New Guinea. Those which range more widely often go no farther than Java, Sumatra, or Borneo; fewer extend to the Philippines or the small islands of the Pacific. The accepted species names are given with their synonyms, a detailed description, a statement of range and detailed distribution within New Guinea, ecological and other notes, and a map and illustration. There is an extensive section on the phytogeography of *Grammitis* in New Guinea, as well as an index to scientific names and an index to collections. —*D.B.L.*

Anti-microbial Activity of Phenolic Acids in Pteridium aquilinum

MICHAEL SAN FRANCISCO and GILLIAN COOPER-DRIVER*

All land plants are continually exposed to a wide variety of microorganisms ranging from those which are beneficial to those which are pathogenic. Most plants remain remarkably healthy, and this seems to be especially true of ferns, which reportedly are rarely subject to diseases (Braid, 1940; Hutchinson, 1976; Bandoni, pers. comm.). It is now generally recognized that the resistance of plants to pathogens (and other predators) is mainly due to their containing fungicidal and bactericidal secondary compounds. The few surveys which have been carried out on ferns have confirmed that they do contain such antibiotic substances (Maruzzella, 1961; Khrisagar & Mehta, 1972; Lynch-Brathwaite et al., 1975; Banerjee & Sen, 1980; Cooper-Driver et al., in prep.).

One major class of secondary compounds with known antimicrobial activity is the phenolics, which range from simple phenols to complex polymeric tannins (Harborne, 1982, pp. 230–264). Their main role in plants appears to be as protective compounds against fungi, bacteria, and viruses (Friend, 1979; Swain, 1979). For example, the flavonoids present in the farinose exudate on the leaf surfaces of some ferns have antimicrobial properties (Chowdhury et al., 1974; Wollenweber, 1978).

Simple phenolics, such as *p*-hydroxybenzoic, protocatechuic, and vanillic (hydroxybenzoic) acids, and *p*-coumaric, caffeic, and ferulic (cinnamic) acids *(Fig. 1)* have been shown to be present in the fronds of ferns (Bohm & Tryon, 1967; Bohm, 1968; Cooper-Driver, 1976) and to play an important role in the ecology of Bracken (*Pteridium aquilinum* (L.) Kuhn) by inhibiting the germination and growth of neighboring plants (Stewart, 1975; Glass, 1976; Gliessman & Muller, 1978). Such acids are also known to have inhibitory effects on feeding by insects (Jones & Firn, 1979). The concentration of these acids in the leaves is known to vary quantitatively during growth and development (Glass & Bohm, 1969; Cooper-Driver et al., 1977; Jones, 1983), and thus must affect the antimicrobial, allelopathic, and anti-insecticidal properties of the plants differentially during the growing season.

Simple phenolic and cinnamic acids must also play a major role in the defense of fern gametophytes against pathogens, particularly since more complex phenols, such as flavonoids, have been shown to be absent during the pre-antheridial stage (Petersen & Fairbrothers, 1980).

However, it has been reported that fern prothalli are readily susceptible to several species of "damping off" fungi, like *Pythium* species (Gregor, 1938, pp. 141–154), and gametophytes grown in pure culture can be readily invaded by *Botrytis cinerea*, *Pythium debaryanum*, and *Rhizoctonia solani* (Hutchinson & Fahim, 1958). Gametophytes grown in pure culture appear to be more susceptible to molds and damping off diseases than to the more specific pathogens of angiosperms, *Fusarium solani* and *Verticillium dahliae* (Hutchinson, 1976). In angiosperms, many of these

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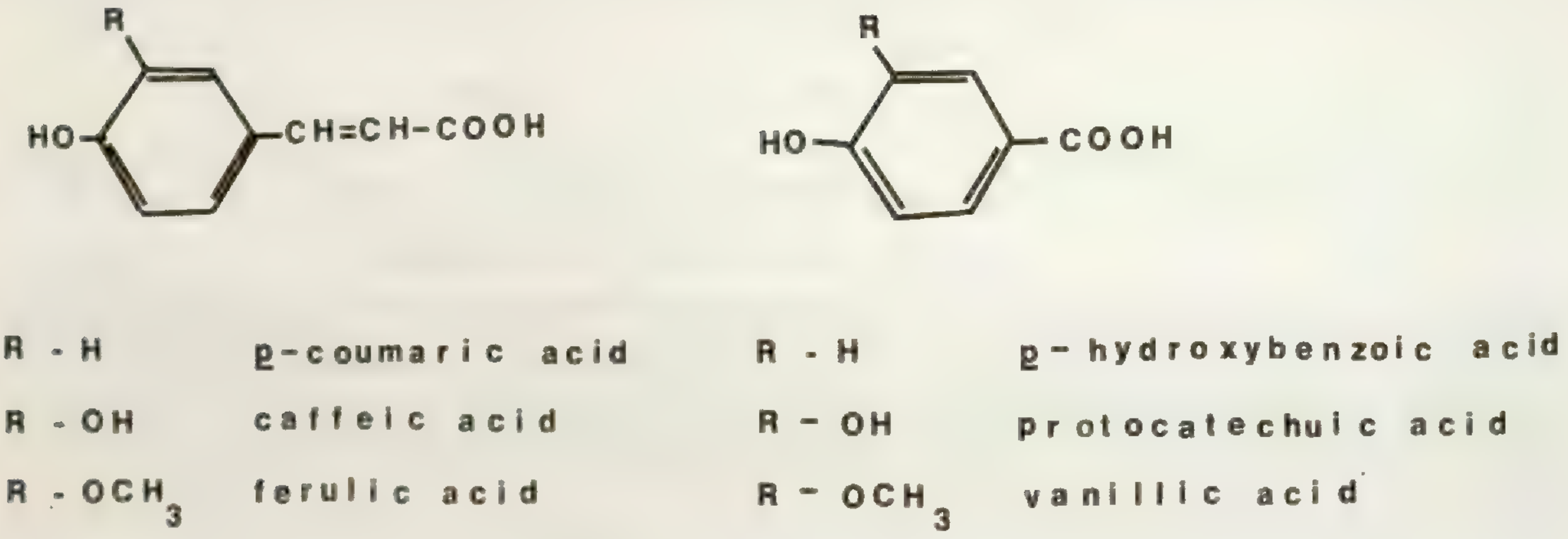

FIG. 1 Commonly occurring phenolic acids in Pteridium aquilinum.

damping off fungi attack only the seedling stage, and plants become progressively more resistant to attack as they mature. Infections are most severe at high moisture levels. These pathogens survive for relatively long periods in the soil (Wheeler, 1976, pp. 9–27), posing a potential threat to fern gametophytes.

It was of interest, therefore, to investigate the effect of the concentration of phenolic acids isolated and identified from the gametophytes and sporophytes of Bracken on the growth of fungal and bacterial plant pathogens. All nine organisms tested, with the exception of *Erwinia*, have been reported to cause infections of Bracken (Gregor, 1938; Hutchinson & Fahim, 1958; Hutchinson, 1976). Changes in the concentrations of the acids were measured in Bracken over the May to October growing season, and observations were made of visible signs of fungal infections. We also isolated fungi and bacteria at frequent intervals throughout the year.

MATERIALS AND METHODS

Isolation of phenolic acids from gametophytes.–Spores of *Pteridium aquilinum* were collected in August and following sterilization (Haufler, pers. comm.) were sown on an agar slant of Moore's medium (Klekowski, 1969) as a slurry of spores and water. The tubes were incubated at 25° C, 12 hours day length. Germination was observed after approximately 1.5 weeks, and the gametophytes were grown until they were eight weeks old. The 80% methanolic extract of the gametophytes was base hydrolysed, and the acids were separated by thin layer chromatography (TLC) on cellulose using benzene-acetic acid-water (6:7:3, upper phase) in one direction and 1N sodium hydroxide–formic acid–water (150:8:42) in the second direction. The acids were detected by spraying with diazotized sulfanillic acid. Gametophytes were subcultured 7 to 8 weeks following inoculation, which proved to be a good method for increasing the amount of gametophyte tissue and also for initiating antheridium formation and subsequent sporophyte growth.

The quantification of phenolic acids present in the gametophyte tissue was carried out by direct extraction with 80% methanol and by base hydrolysis with 2N NaOH for 2 hours under nitrogen followed by acidification, extraction of the released acids with ether, purification via re-extraction into sodium bicarbonate, acidification, and final extraction into ether. The solution was then evaporated to dryness and the residue taken up in a few drops of methanol. Absorbance was read at 310nm and related to known concentrations of *p*-coumaric acid as a standard. The methanol-insoluble residue was also base hydrolysed and examined for the presence of phenolic acids.

Isolation of phenolic acids from sporophytes.–Dried material was extracted with 80% methanol. The extract was base hydrolysed as described above and the free acids separated by thin layer chromatography using the solvent systems isopropanol–*t*-butanol–*n*-butanol–ammonia–water (4:2:2:1:2) in the first direction, followed by benzene–acetic acid–water (6:7:3, upper phase) in the second direction. Both R_F values of the acids and their ultra-violet spectral properties were compared with standards (Cooper-Driver et al., 1972).

Quantitative estimates were made on dried samples of Bracken collected from three sites of the Massachusetts Audubon Bird Sanctuary at Natick at bi-weekly intervals. The procedures used for the quantification of the phenolic acids were identical to those described above for the gametophytes.

Micro-organisms.–Test organisms included the fungi *Botrytis cinerea*, *Rhizoctonia solani* (Deuteromycetes), *Pythium debaryanum*, *P. middletonii*, and *P. ultimum* (Oomycetes) and the bacteria *Corynebacterium poinsettiae*, *C. fasciens*, *Erwinia amylovora*, and *E. carotovora*. The *Erwinia* species were chosen as examples of economically important pathogens as causal agents of fireblight disease (Quamme et al., 1976). Cultures of *B. cinerea* and *R. solani* were obtained from the American Type Culture Collection and the *Pythium* cultures from Dr. C. Bracker, Purdue University. The *Corynebacterium* species were obtained from Dr. M. Starr, University of California, Davis, and the *Erwinia* from Dr. A. Chatterjee, University of Kansas.

Fungal cultures were maintained on potato dextrose agar (PDA) at 27° C, and phenolic acids were added to the plates either singly or in combination to give final concentrations of 0.005%(50ppm), 0.01%(100ppm), 0.05%(500ppm) and 0.1% (1000ppm) w/v. The plates were inoculated with cultures of fungi, by inversion, and were incubated for 5 days at 27° C. Fungal growth was measured and expressed as the extent of hyphal growth as a percentage of the control (without added acid). All tests were run in triplicate.

Bacteria were grown in nutrient broth. Phenolic acids were added either individually or in combination in order to give final concentrations of 0.005%(50ppm), 0.01%(100ppm), 0.05%(500ppm) and 0.1%(1000ppm) w/v. The medium was first autoclaved and then inoculated with 2×10^{-5} bacteria in exponential growth (10^6 cells per ml); bacterial growth was measured by determining the absorption at 580nm and was expressed as a percentage of the control (Khrisagar & Mehta, 1972).

Microbial infections.–Field observations on microbial infections were made on 20 labelled Bracken plants at bi-weekly intervals. Typical signs of infection were

TABLE 1. MINIMUM CONCENTRATION OF PHENOLIC ACIDS (In ppm) CAUSING 50% INHIBITION OF FUNGAL OR BACTERIAL GROWTH.

Fungi	*p*-coumaric	ferulic	caffeic	*p*-hydroxybenzoic acid	vanillic	protocatechuic	combination of all acids
Rhizoctonia solani	50	50	100	100	›1000	›1000[1]	100
Botrytis cinerea	500	500	›1000	›1000	›1000[1]	›1000[1]	500
Pythium debaryanum	100	500	500	500	500	1000	50
P. middletonii	50	50	50	50	50	50	50
P. ultimum	50	50	100	100	500	›1000[1]	50
Bacteria							
Corynebacterium poinsettiae	100	500	1000	1000	500	100	50
C. fasciens	500	500	100	500	500	1000	50
Erwinia amylovora	50	50	100	50	50	50	100
E. carotovora	100	50	100	50	100	100	50

[1]stimulatory at low concentrations

local necroses, indicated as leaf spots or brown necrotic tissue especially around damaged areas, and 'Curl-tip', which was shown by curling and darkening at the apex of the pinnae. The amount of infected tissue was estimated.

In order to isolate micro-organisms from infected plant tissue, the tissue was surface sterilized with 1 ppm mercuric chloride and washed in 70% ethanol followed by sterilized distilled water. The tissue was dried and placed on suitable growth medium, PDA for isolation of fungi and nutrient agar (NA) for bacteria. Plates were incubated at 30° C. Seventeen different bacteria and eight fungi were isolated from infected areas and obtained in pure culture. Attempts were made to demonstrate the pathogenicity of these fungi, but it was difficult to demonstrate re-infection of Bracken plants in the field (cf. Hutchinson, 1976), either by inoculating the leaf surface by scraping or by injecting the stem at the junction of the petiole and the stem.

RESULTS

Bracken gametophyte tissue was surprisingly completely devoid of flavonoids. The major phenolic compounds present were *p*-coumaric, caffeic, ferulic acids, and *p*-hydroxybenzoic acid; vanillic, protocatechuic, and *o*-coumaric acids, which were present in the sporophyte, could not be detected. There were few qualitative or quantitative changes in these acids in the gametophytes from one week up to ten weeks. The acids were present mainly as glucose or quinic acid esters, and electrophoresis at pH 2.2 and treatment with sulfatase confirmed the presence of

sulfated derivatives of caffeic and *p*-coumaric acids (Cooper-Driver & Swain, 1975). Phenolic acids in the gametophytes were present at concentrations of 0.15–0.20%/gm dry weight. Base hydrolysis of the alcohol-insoluble fraction gave no indication that hydroxy-cinnamic acids were bound to the cell walls (Hartley & Jones, 1977), whereas *p*-coumaric and ferulic acids were isolated from the base hydrolysate of the methanol insoluble residue of the sporophyte.

No flavonoids were detected in sporophytes growing from the gametophytes, whereas vegetatively produced sporophyte plants on emergence synthesized flavonoid glycosides.

The effect of these acids on the growth of *Botrytis cinerea*, *Rhizoctonia solani*, and *Pythium* species, together with *Corynebacterium poinsettiae*, *C. fasciens*, and *Erwinia* species is shown in *Table 1* and is expressed as minimum concentrations of acids causing 50% inhibition of fungal or bacterial growth. Overall, cinnamic acids, especially ferulic and *p*-coumaric acids, were the most effective inhibitors of fungal growth (the growth of *Rhizoctonia solani* was inhibited at concentrations as low as 50ppm). On the other hand, protocatechuic acid was stimulatory to growth of *R. solani* at all concentrations tested, and vanillic acid was only slightly inhibitory (18%) at concentrations as high as 1000ppm. In the case of *Botrytis cinerea*, the hydroxybenzoic acids together with caffeic acid had little effect on growth, and *p*-coumaric and ferulic only inhibited growth at concentrations of 500ppm or above, and then only by 55%. In combination, the acids were inhibitory to growth of *R. solani* at 100ppm (50%) and were completely inhibitory to growth at higher concentrations. For *B. cinerea*, 500ppm was inhibitory (74%), and no growth occurred at higher concentrations. Overall, however, *R. solani* was much more affected by phenolics than was *B. cinerea*.

All *Pythium* species also showed much greater susceptibility to phenolic acids than did *Botrytis*. Growth of *P. debaryanum* was uniformly inhibited by phenolic acids at concentrations above 500ppm, and 100ppm ferulic acid and *p*-coumaric acid inhibited growth 13% and 50% respectively. Protocatechuic acid was the least inhibitory. The growth of *P. middletonii* was inhibited at all concentrations of the acids tested, whereas the growth of *P. ultimum* was stimulated by protocatechuic acid. In all *Pythium* species, no growth occurred when a combination of acids was added to the medium.

The bacterial species tested responded to the phenolic acids in a more uniform manner. At 50ppm, the acids were mildly stimulatory or caused only slight inhibition of growth (<25%). As the acid concentration increased, there was a corresponding increase in inhibition. There were no differences in the inhibitory action of hydroxybenzoic acids or cinnamic acids. Combinations of the acids inhibited bacterial growth in all cases. No growth was observed at concentrations above 100ppm and, with the exception of *E. amylovora*, 98% inhibition was observed at concentrations as low as 50ppm.

Seasonal changes in the concentration of phenolic acids in Bracken are shown in *Fig. 2*. There was a slight increase during May, the period of leaf expansion, followed by a slight drop and a gradual increase reaching a maximum concentration of 0.75% phenolic acids/gm dry weight of leaf material (0.25%/gm fresh weight) in

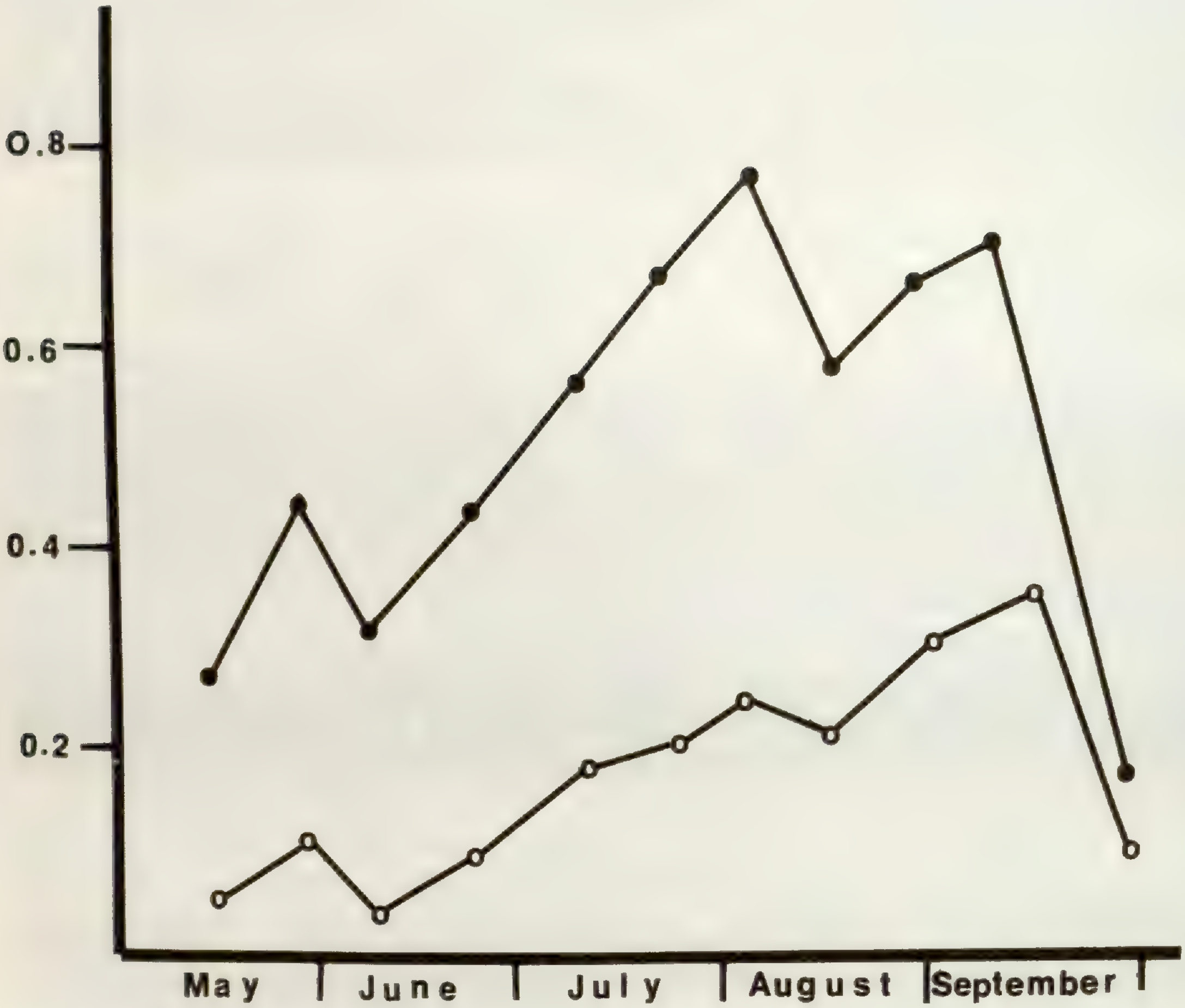

FIG. 2 Seasonal changes in the concentration of phenolic acids (in % per gram of dry weight, ●, and fresh weight, ○) in *Pteridium aquilinum* leaves.

late July. There was then a drop in phenolic acid concentrations during August following a period of heavy precipitation (1.2 in rain) that caused leaching of the acids from the leaves. The concentration of phenolic acids in the leaf tissue dropped markedly as senescence set in during September and October.

The number of fungal and bacterial species isolated from sterile leaf tissue showed a general increase as the fronds matured, with an especially sharp increase in the amount of infected tissue in early August.

DISCUSSION AND CONCLUSION

Phenolic acids, when added to a microbial growth medium, inhibit the growth of both fungi and bacteria. They have been shown to react with fungal enzymes and other proteins. Phenolic compounds in infected tissues are often oxidized and polymerize to form reactive oligomeric products that may have increased antimicrobial activity often associated with increased inhibition of the cell wall degradation caused by extracellular enzymes produced by pathogens (Friend, 1979). This may account for the high inhibition of *Rhizoctonia solani* by phenolic acids, as

oxidation products were seen as brown rings around the edges of the fungal mycelium. Hunter (1974) has demonstrated that the resistance of cotton plants to *R. solani* is due to oxidized catechin, which inhibits the polygalacturonase activity of the pathogen. Phenolic acids also act on membrane permeability and electric potentials, causing an enhanced ratio of oxygen consumption by uncoupling electron transfer (Glass & Dunlop, 1974).

The variation in response of the fungi, *Botrytis* and *Pythium* to phenolic acids may be a reflection of the chemical composition of their cell walls. Chitin is known to be far more resistant to microbial decomposition than is cellulose (LeJohn, 1971). This may explain the relative resistance of *Botrytis* over *Pythium* species to the phenolic acids, as *Rhizoctonia* and *Botrytis* have cell walls of chitin, whereas those of *Pythium* are composed primarily of cellulose (Bartnicki-Garcia, 1968). Cell membranes of *Pythium* also lack sterols, which are present in both species of Deuteromycetes (Hall, 1979). Differences in cell wall composition between the two genera of bacteria (Stanier et al., 1976, p. 871) are not reflected in their response to the individual acids. The high resistance of *B. cinerea* to phenolic acids is interesting in light of the fact that this fungus has often been found associated with Bracken. Godfrey (1974) reported *B. cinerea* on the leaf surface (phylloplane); we also found this species to be present in leaf isolates. In addition, *B. cinerea* has been recorded on decomposing Bracken petioles (Frankland, 1976), and prothalli are also very susceptible to attack by this organism (Hutchinson, 1976).

It is also interesting that the cinnamic acids, ferulic and *p*-coumaric, are generally the most inhibitory acids to the growth of fungi and bacteria. The cinnamic acids are of prime importance in lignin formation, and polysaccharide esters of *p*-coumaric and ferulic acids have been shown to be released from the cell walls of grasses by cellulase action (Hartley & Jones, 1977). It has been suggested that such acetylation of the cell wall polysaccharides by hydroxycinnamic acids may be a primitive mechanism to protect plants from fungi and other micro-organisms (Swain, 1979). Although gametophytes do not have bound cinnamic acids in their cell walls, as shown by the lack of detectable acids in the hydrolysed residue, nevertheless these compounds were present in the soluble fraction and were the most effective anti-microbial compounds against the pathogenic organisms tested.

Mixtures of simple phenolic acids have a synergistic effect and are better inhibitors of microbial growth when present in combination. These same acids have also been shown by Adams and Bernays (1978) to be more effective deterrents to feeding by *Locusta migratoria* in combination. Increased synergistic inhibitory effects of acids on radish and sorghum germination have also been shown (Rasmussen & Einhellig, 1977; Einhellig & Rasmussen, 1978).

From the field and laboratory studies, it was evident that phenolic acids are present in high enough concentrations in Bracken sporophytes (0.25–0.75%, 4500–7500ppm, phenolic acids/gm dry weight) and gametophytes (0.15–0.20%, 1500–2000ppm, phenolic acids/gm dry weight) to play an important role as antimicrobial compounds. Damage to the tissues by the invading microorganisms releases the acid esters as free acids (Woodhead & Cooper-Driver, 1979). Since phenolic acids are effective inhibitors of microbial growth at concentrations of the

order of 100ppm w/v, they obviously play an important anti-microbial role in Bracken. The concentration of phenolic acids present in gametophyte tissue was much lower, but was still high enough to inhibit microbial growth.

Concentrations of phenolic acids in the leaves of *Pteridium aquilinum* changed over the season depending not only on the age of the plant, but also on abiotic and biotic factors. The sharp increase in infected tissue and the numbers of isolated microorganisms detectable in early August may be due to a preceding period of heavy precipitation followed by warm, humid weather around 40° C. The heavy rainfall would have resulted in leaching of the phenolic acids from the leaves, and thus a decrease in chemical protection. In July there was a heavy infestation of aphids on the Bracken fronds, and the presence of these insects could well have increased the points of entry for the fungal hyphae, as well as promoting greater leaching of plant defense chemicals from the leaves.

A comparison of phenolic compounds in sporophytes and gametophytes of *Polypodium aureum*, *Thelypteris patens*, *T. normalis*, *Asplenium aethiopicum*, *Cyrtomium falcatum*, *Gymnopteris rufa*, and *Pteris straminea* (Cooper-Driver, unpubl.) has shown that there are two distinct patterns: (a) ferns in which the phenolic complement in gametophytes and sporophytes is identical with often a wide range of flavonoids being present in both, and (b) those in which the phenolics in the gametophyte are restricted to simple phenolic acids, as in the present case of Bracken. It is interesting to speculate whether this difference in gametophyte chemistry reflects the dependence of the species on the gametophyte for reproduction. As is well known, Bracken reproduces mainly vegetatively.

Thus it has been shown that phenolic acids differentially inhibit the growth of fern pathogens and other bacteria *in vitro* and are present for most of the growing season in high enough concentrations *in vivo* in the plant tissues to inhibit the growth of pathogenic microbes.

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REVIEW

The Phylogeny and Classification of the Ferns, A. C. Jermy, J. A. Crabbe, and B. A. Thomas, eds. Koeltz Scientific Books. 284 pp. Reprint 1984. DM150 (ca. $60.00).—This authorized reprint makes available again the results of the Symposium on the Phylogeny and Classification of the Filicopsida, which was held in London in April 1972. The original volume was reviewed by C. Page (Fern Gaz. 11:47–48. 1974). The reprint is on slightly thinner and less opaque paper than is the original and there is a slight but inevitable loss in definition of the photographic illustrations, but the volume is sturdily bound and fully serviceable, and will make an excellent addition to any fern student's library.—*D.B.L.*

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The Identification of Hawaiian Tree Ferns of the Genus Cibotium

RICH BECKER*

The identification of Hawaiian tree ferns is difficult for most laymen and taxonomists because of past nomenclatural confusion, misapplication of the specific names, and the absence of a complete key to all of the species. Although *Sadleria*, a Hawaiian endemic genus of the Blechnaceae, has some arborescent species which are referred to as tree ferns, these are not treated in this paper. The correct nomenclature of the six *Cibotium* species found in Hawaii is presented. A simple key is given for the species. This is supplemented with descriptions of their characteristics as seen in their native habitats. I have deposited in the herbarium of the University of Hawaii my reference collection of entire fronds for each of the Hawaiian species described.

The range of *Cibotium* extends from Assam through China, Malaya, Indonesia, the Philippine Islands, and Hawaii to southern Mexico and Guatemala. There are three Asiatic species (Holttum, 1963, pp. 164–166).: *C. barometz* (L.) J. Smith, *C. cumingii* Kunze, and *C. arachnoideum* (C. Chr.) Holttum. The Central American species are: *C. schiedei* Schlecht. & Cham. (Mexico), *C. regale* Versch. & Lem. (Mexico to Honduras), and *C. wendlandii* Mett. ex Kuhn (Mexico and Guatemala), according to Smith (1981, pp. 75–76) and Stolze (1976, pp. 94–97).

The six endemic Hawaiian *Cibotium* species are: *C. glaucum* (J.E. Smith) Hook. & Arn., *C. chamissoi* Kaulf., *C. splendens* (Gaud.) Krajina ex Skottsb., *C. nealiae* Degener in Degener & Hatheway, *C. hawaiense* Nakai & Ogura in Ogura, and *C. st.-johnii* Krajina. *Cibotium glaucum* and *C. chamissoi* are found in the rain forest areas of Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii. *Cibotium splendens* is common on Oahu; forms of it may also be on Molokai and Maui, but this has not been confirmed. *Cibotium nealiae* and *C. st.-johnii* are apparently restricted to Kauai. *Cibotium hawaiense* is endemic to the island of Hawaii; it is locally abundant on that island. I have seen it close to Wright Road in the Olaa Forest, at Puu Makaala near the Stainback Highway, at the end of the Olaa Back Road, above Laupahoehoe, and in the Kohala Mountains. The most common species on the island of Hawaii is *C. glaucum*. *Cibotium chamissoi* is the next most abundant.

The key to resolving the nomenclatural confusion associated with the Hawaiian tree ferns lies in understanding Hooker's treatment of the genus in the *Species Filicum* (1844). He separated *C. chamissoi* Kaulf. and *C. glaucum* (J.E. Smith) Hook. & Arn. and described a new species, *C. menziesii* Hook. Krajina in Skottsberg (1942, pp. 30–41) showed the latter to be identical to *C. chamissoi* Kaulf. and the name *C. chamissoi sensu* Hooker to be *C. splendens* (Gaud.) Krajina ex Skottsb.

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Hillebrand may have used the name *C. chamissoi* Kaulf. in its original sense on some of his first collection labels (Skottsberg, 1942, p. 40). However, in the *Flora of the Hawaiian Islands*, Hillebrand (1888, pp. 545–548) used the incorrect nomenclature from Hooker's *Species Filicum*, as did Rock (1913), in his *The Indigenous Trees of the Hawaiian Islands*. Both are standard works on the Hawaiian flora that were for a long time assumed to be correct, causing many later authors to unwittingly use an incorrect nomenclature. The credit for uncovering the synonymy belongs to Krajina, who has carefully studied the genus.

The key given below is based on relatively constant characteristics that are easily observable in the field on mature plants. Other characteristics, such as trunk height, frond length, pinnule width, and number of sori per pinnule, vary greatly with the age and vigor of the plants. They are not reliable diagnostic features and have not been used in the key.

KEY TO THE HAWAIIAN SPECIES OF CIBOTIUM

1. Stipes with reddish-brown or stiff purplish-black hairs along most of their length.
   2. Fronds distinctly glaucous beneath; costae villosulous .....1. *C. st.-johnii*
   2. Fronds not glaucous beneath; costae glabrous .....2. *C. chamissoi*
1. Stipes naked, or with dull brown or golden brown hairs mainly at their base.
   2. One or both of the basal pinnule segments auriculate, fronds glabrous and distinctly glaucous. 3. *C. glaucum*
   2. None of the pinnule segments auriculate; fronds not or only slightly glaucous beneath.
      3. Stipes very dark brown to blackish with a conspicuous, white line along each side when fresh; pinnule segments covered with tufts of hairs (as seen under 10× lens) beneath .....4. *C. nealiae*
      3. Stipes brown or greenish when fresh; pinnule segments covered with cobweb-like hairs (as seen under 10× lens) beneath.
         4. Trunk slender and smooth, stipes covered with inconspicuous, soft, matted, dull, brown hairs. 5. *C. hawaiense*
         4. Trunks rough with stubs of dead fronds; stipe bases with golden brown hairs 6. *C. splendens*

1. Cibotium st.-johnii Krajina, Stud. Bot. Čechosl. 1(2):94. 1938.

The most characteristic feature of *C. st.-johnii* is the copious amount of matted hairs on the full length of the stipes, and on the costae and costules. The hairs at the base of the stipes are, when fresh, reddish-brown. Further up the stipes and on the costae they are grayish-brown to whitish. *Cibotium st.-johnii* closely resembles *C. glaucum*, but has much smaller fronds. In 1966, Dr. Krajina annotated *Heller 2818* (BISH 01703, 01703a 01703b) as "*Cibotium glaucum* (Sm.) H. & A. subsp. *St.-Johnii* (Krajina) c.n. var. *fallax* Krajina." The description of Hillebrand's (1888, p. 547). *C. chamissoi* var. β can be used to confirm the identity of *C. st.-johnii*. *Distribution: Alakai swamp, Kauai.*

2. Cibotium chamissoi Kaulf. Berl. Jahrb. Pharm. 21:53. 1820.

C. menziesii Hook. Sp. Fil. 1:84, *t. 29C*. 1844.

This is the most robust species. The stipe bases are covered with long, reddish-brown hairs; further up the stipe, the hairs are still and blackish. The rachis and the costae are often straw-colored. The fronds are not at all glaucous beneath and usually are glabrous, but sometimes have minute, scattered tufts of hairs visible under 40× magnification. Distribution: Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii. Hawaiian name: hapu'u'i'i.

On the islands of Molokai, Lanai, and Hawaii, I have seen several tree ferns that may be hybrids between *C. glaucum* and *C. chamissoi*. Their fronds were distinctly glaucous beneath and their basal pinnule segments auriculate. These are characteristics of *C. glaucum;* however, their stipe hairs were bristly and either dark purplish-brown or dark orangy-brown.

3. Cibotium glaucum (J. E. Smith) Hook & Arn. Bot. Beech. Voy. 3:108. 1832.

Dicksonia glauca J.E. Smith, Rees' Cyclop. 11(22). 1808.

Cibotium glaucum is the most abundant species on the Island of Hawaii. The stipe bases are covered with a mass of glossy, golden-yellow hairs and are lustrous when dry. The distal part of the stipes and the rachis are essentially naked. The fronds are glabrous and bright glaucous beneath (slightly less so in the wetter parts of the range of the species). The pinnule segments closest to the costae are auriculate and overlap the costae. The auricles are largest on plants from the island of Hawaii; they are present but much smaller on plant forms from the other islands. One plant I examined on Molokai had one frond exauriculate. In this species, the stipe bases remain attached to the trunks for some time after dead fronds drop off. Distribution: Kauai, Oahu, Molokai, Lanai, Maui, and Hawaii. Hawaiian name: hapu'u pulu.

4. Cibotium nealiae Degener in Degener & Hatheway, Fl. Haw. 5: Family 12. 1951.

The stipe bases of this species are very dark brown, almost black, and are covered with a thick mass of matted, yellowish hairs. Distally, the stipes are greener and naked. A conspicuous, long, white line (pneumatothode) extends along each side of the fresh stipes. I found the pneumatothodes to be very obvious when I saw the species in the field. Although the lines are a useful field identification, they did not remain visible on my herbarium specimens. The costules and veins are yellow and prominent. The frond underside is green, but not glaucous beneath. The costules are covered with very small tufts of hairs beneath. Distribution: Hanalei, Kauai.

5. Cibotium hawaiense Nakai & Ogura in Ogura, Bot. Mag. Tokyo 44:468. 1930.

The spelling of the epithet *hawaiense* follows Nakai and Ogura's original publication. The stipes of *C. hawaiense* may appear naked, but actually are covered with thick, flaky mats of dull brown hairs. When a stipe is pulled back from the trunk, the basal part is seen to be covered with golden, glossy, and slightly lustrous hairs. The laminae are thin and bright green; the underside is slightly paler and somewhat glaucescent. Fine, cobwebby hairs can be seen, with a 10× hand lens, on the undersides of the pinnules. The trunk is slender, and the fronds, after arching upwards, are held almost horizontally. The dead fronds hang down close to the trunk, similar to those of the Date Palm. Eventually they break away cleanly, leaving a smooth trunk. Distribution: Olaa, Laupahoehoe, Kohala Mountains, Hawaii. Hawaiian name: meu.

6. Cibotium splendens (Gaud.) Krajina ex Skottsb. Acta Horti Gothob. 15:40. 1942.

Pinonia splendens Gaud. in Freyc. Voy. Uranie 96, 369, *t. 21*. 1827.

Cibotium chamissoi sensu Hook. Sp. Fil. 1:83. 1844.

This is the most delicate appearing species. It has been confused with *C. hawaiense*, although their ranges do not overlap. A glaucescent form from Molokai (*Fosberg 9600*, BISH 01741) was annotated with the unpublished name *C. splendens* var. *glaucescens* by Krajina. This specimen has pinnule segments that are somewhat glaucous and with arachnoid hairs on their undersides. Distribution: Oahu, and perhaps also on Molokai, and Maui, but not seen by me on these islands, or on Lanai or Hawaii.

I wish to thank Sandra Becker for her assistance in mounting my reference collection of herbarium specimens. The review of the preliminary draft and discussion on the nomenclature of *C. nealiae* by Dr. V. J. Krajina were most helpful. The continued encouragement and support of Drs. D. Mueller-Dombois, K. W. Bridges, and C. Lamoureux, are much appreciated.

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Two New Tree Ferns from Panama

ROBERT G. STOLZE*

Recently I was sent two specimens of tree ferns to identify, which were thought to be *Cnemidaria:* one by Henk van der Werff at the Missouri Botanical Garden, and another by David Lellinger at the U.S. National Herbarium, which was a duplicate he had received from Missouri. One proved to be new species of *Cnemidaria,* the other a new, simply pinnate *Trichipteris*. I am always hesitant to describe new species based only upon single collections, as is the case with these, but each is highly distinctive from others in their respective genera. It is curious that both of these new Panamanian species collected between 1975 and 1982 are very small (for tree ferns) and are simply pinnate.

Cnemidaria glandulosa Stolze, sp. nov. **Fig. 1.**

Folium pinnatum, tenuiter herbaceum, ca. 130 cm longum, 25 cm latum, segmento apicali non conformi; petiolus haud spinosus, petioli paleis abundantibus, bicoloribus; lamina in pagina abaxiali dense glandulosa; glandes minutae, bacilliformes; rhachis plus minusve nuda; pinnae subsessiles, breviter attenuatae, margine integro et revoluto; venae 2- vel 3-furcatae, liberae, vel raro venae basales anastomosantes et areolas costales efformantes; indusium atrobrunneum, plus minusve semicirculare; receptaculum ovideum, sine paraphysibus.

TYPE: North of San Felix at Chiriquí–Bocas del Toro border, on Cerro Colorado copper mine road along continental divide. Lower montane rain forest, 5,000–5,500 ft, Province of Chiriquí, Panama, *Mori & Kallunki 5908* (US; isotype MO).

Thus far known only from the type collection.

Caudex not seen; leaf pinnate, thin-herbaceous, to 130 cm long and 25 cm broad, abruptly terminating in a nonconform apical section (*i.e.* broader at base than the pinnae and with at least one adnate basal lobe); petiole light or yellowish brown, to 45 cm long, lacking spines, the scales abundant, bicolorous, brown with broad, whitish, erose margins, to 1.5 cm long, also sparsely to moderately provided with minute (0.5 mm), appressed trichomes; rachis essentially naked, or with a few scattered scales or trichomes abaxially near the lamina base, slightly alate near the apex; pinnae about 12 pairs, subsessile, the margins entire and revolute, rounded or broadly cuneate at the base, short-attenuate at the apex, the veins and the tissue between rather densely glandular abaxially, the glands dark brown, minute, appressed, bacilliform; costae naked adaxially, sparsely provided with broad, flaccid, amorphous, whitish to tawny scales abaxially; veins 2–3-forked, essentially free, but occasionally merging to form costal areoles, even less frequently merging toward the pinna margin; sori in 1 or 2 irregular lines about midway between costa and margin; indusia dark brown, more or less semicircular, subentire; receptacle ovoid, lacking paraphyses; spores pale yellow to dirty white, globose-tetrahedral, trilete, with one large aperture near the center of each face near the equator.

The new species bears closest resemblance to *C. decurrens* of Mexico and northern Central America, especially in that some forms of the latter have nearly entire pinnae. However, in *C. decurrens* the lamina is eglandular and more gradually reduced to the apex, veins commonly (not rarely) merge to form costal areoles, and the indusia are pale or yellowish (not dark) brown. The occurrence of numerous

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FIG. 1. Holotype of Cnemidaria glandulosa, *Mori & Kallunki 5908* (US).

glands on the abaxial surface of pinnae is unique in the genus. In *C. glandulosa* the glands may be observed even at low magnification, and by using higher power (25×) one can easily discern their rod-like shape.

FIG. 2. Holotype of Trichipteris pinnata, *Knapp 5881* (MO).

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Fig. 2.

Trichipteris pinnata Stolze, sp. nov.

Folium pinnatum, tenuiter vel firme herbaceum, circa 50 cm longum, 20 cm latum, segmento apicali conformi, segmentum apicale ad basim articulatum; petiolus haud

spinosus vel interdum sparse muricatus, squamis ovatis vel lanceolatis, nitidis, brunneis vel interdum bicoloribus; pinnae nonnullae, breviter petiolulatae, ad rhachim articulatae, margine crenato, in pagina abaxiali dense glandulosae; costae in pagina abaxiali glabrae, adaxialiter strigosae; indusium nullum; receptaculum globosum, paraphysibus brevibus.

TYPE: Santa Rita Ridge road, 21–26 km from Transisthmian Highway. Tropical wet forest, 500–550 m, Province of Colón, Panama, *Knapp 5881* (MO; isotype F).

Thus far known only from the type collection.

Caudex erect, ca. 6 cm long, 1 cm broad; leaf pinnate, thin- to firm-herbaceous, to 50 cm long and 20 cm broad, abruptly terminating in a conform apical segment which is articulate at the base; petiole 18–22 cm long, yellowish or grayish brown, lacking spines, but sometimes slightly muricate, amply scaly at least near the base, the scales 5–7 cm long, ovate to lanceolate, lustrous brown or some of them bicolorous (with narrow, whitish margins); rachis naked abaxially, or with a few brown scales, densely provided with minute, terete, appressed trichomes on the adaxial side; pinnae several pairs, short-stalked, articulate to the rachis, the margins crenate, the apex acuminate, the base subtruncate to broadly rounded, the tissue between the veins rather densely gland-dotted on the abaxial side; costae glabrous abaxially, densely provided with appressed trichomes as on the rachis adaxially; veins 4–6 pairs along the costule, only the distal ones reaching the pinna margin; sori borne on the proximal 1/3 or 1/4 of each vein branch; indusia lacking; receptacle globose, with short paraphyses among the sporangia; spores pale yellow to whitish, trilete, rather sharply tetrahedral.

Compared to most tree ferns, this is a very diminutive one—the fronds are only half a meter long and the caudex is small, not trunk-like. Of course, it must be expected that as more collections are made of this species, much larger plants also may be found. *Trichipteris pinnata* is most likely to be confused with *T. williamsii* Maxon of Panama, Colombia, and Venezuela, one of two species in the genus with entire or subentire pinnae (*Trichipteris* typically has huge leaves, 2–3-pinnate or more). Both species also have the lamina abruptly terminating in a conform apical segment which is articulate to the rachis, and the lateral pinnae are nodose-articulate as well. In *T. williamsii*, however, the pinnae are subcoriaceous, with their margins entire, or at best slightly undulate, and the basal veins often or occasionally merge to form costal areoles. Pinnae of *T. pinnata* are thin- to firm-herbaceous, with their margins rather deeply crenate and veins are all free. Leaf tissue in *T. williamsii* is eglandular, whereas the abaxial surface of the pinnae in *T. pinnata* is copiously dotted with minute, castaneous glands.

There is some disagreement about the valid spelling of the name *Trichipteris*, some authors preferring "*Trichopteris*." Tryon (1970, p. 41) adhered to Presl's original spelling, as did Barrington (1978, p. 19) in his revision of the genus. Holttum and Edwards (1983, p. 161) and others prefer to adopt Schott's alteration to "*Trichopteris*" for orthographic reasons. I do not intend here to belabor either argument, as the rules according to the I. C. B. N. are rather ambiguous and/or flexible in cases of this kind. I prefer to follow Tryon, who separated the many species of *Trichipteris* from *Alsophila*, and Barrington, who did the revision.

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Trunk Length and Frond Size in a Population of Nephelea tryoniana from El Salvador

Ralph L. Seiler*

Field observations of tree fern fronds suggested that small tree ferns have longer stipes relative to lamina length than tall tree ferns of the same species. This study was done to determine how total frond length, lamina length and stipe length vary within a population.

In April 1979, measurements were made of 146 fronds on 45 individuals of *Nephelea tryoniana* Gastony from a dense cloud forest at 2250 m in Bosque Montecristo, a wildlife preserve in northwest El Salvador. The forest is described more completely in Seiler (1981). The trunk length of each tree was measured, as well as the stipe and lamina length of all undamaged fronds. Usually three fronds per tree were measured, but occasionally four or five or as few as two per tree were measured. The majority of the fronds were sterile, but the presence of fertile fronds should have no effect on the results, for fertile and sterile leaves are practically monomorphic in *Nephelea* (Gastony, 1973).

RESULTS

The length of the fronds of a tree is fairly constant. The standard deviation within a tree averaged 4.55% ($s=2.96$, $n=45$). Analysis of 139 fronds on 43 trees indicates frond length is weakly related to trunk length ($r=0.39$, $P<0.01$). Two of the 45 trees were not included in the statistical analysis for reasons that will be discussed later. In *Figure 1*, frond length is plotted against trunk length. Each point represents the mean frond length from one tree.

The ratio of lamina length to stipe length within a tree is also fairly constant; the standard deviation within a tree averaged 5.72% ($s=3.01$, $n=45$). Analysis of 139 fronds on 43 trees indicates that shorter tree ferns do have longer stipes relative to lamina length and that the lamina/stipe ratio is strongly correlated to trunk length ($r=0.90$, $P<0.01$). In *Figure 2* the ratio of the lamina length divided by the stipe length is plotted against the trunk length; each point represents the mean lamina/stipe ratio for one tree.

Two trees, numbers 17 and 22 (*Figs. 1* and *2*), were found that had been knocked over and, although the main trunks were covered with humus and litter, the crowns had subsequently turned and grown upright. Usually the trunk length is more or less equal to the height of the crown above the ground, but in both of these trees the actual height of the crown was more than a meter less than the length of the trunk. The data gathered from these two trees were not included in the statistical analyses because these two trees were different from the rest in that the effective height was much less than the trunk length and being forced to change the direction of growth may have had an unknown effect on the apical meristem.

The effective height of the crown is better predicted by the measured lamina/stipe ratio than is the total trunk length on the two fallen trees. In tree 22 the lamina/stipe

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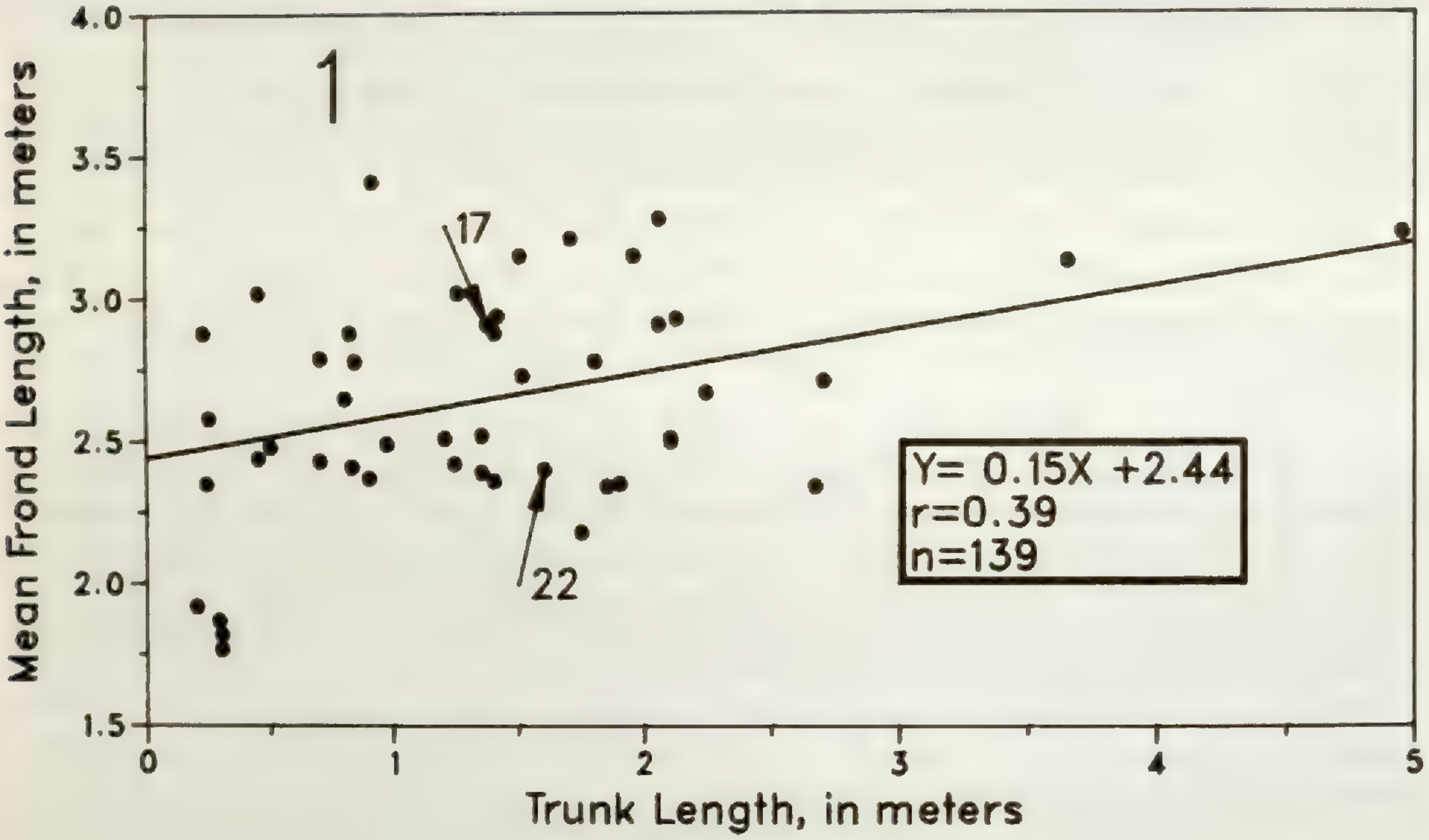

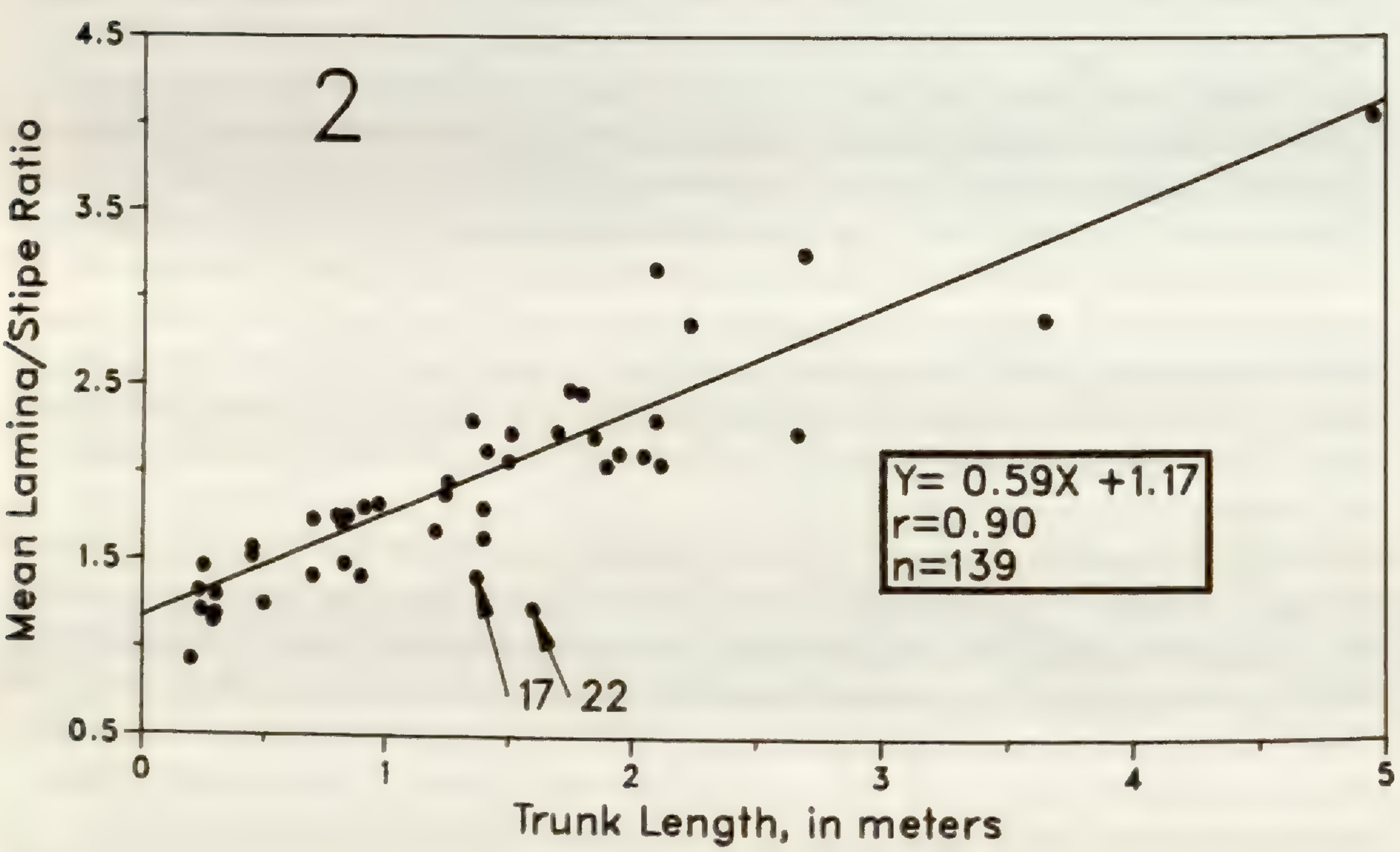

FIG. 1. Relationship between mean frond length and trunk length in *Nephelea tryoniana*. See text for explanation of numbered points. FIG. 2. Relationship between lamina length divided by stipe length (lamina/stipe) and trunk length in *Nephelea tryoniana*. See text for explanation of numbered points.

ratio is 1.23, the trunk length is 160 cm, and the effective height is 16 cm. The predicted trunk length is 10 cm for this tree. Similarly, tree 17 has a lamina/stipe ratio of 1.42, a trunk length of 137 cm, and an effective height of 27 cm. The predicted trunk length is 41 cm.

DISCUSSION

More measurements of trees taller than two meters would have been desirable, but would have required cutting the trees down. Since all tree ferns are very rare in El Salvador and are protected in Bosque Montecristo, only the 5 m tall tree was cut down. The sampling bias towards small trees could cause undue weight to be put on the values for the two tallest trees, suggesting a correlation between frond and trunk length that may not really exist. Omission of the data from the two tallest trees reduces the correlation coefficient; however, the correlation is still significant ($r=0.22$, $P<0.05$).

The lamina/stipe ratio is strongly correlated with the trunk length. The effective height of the crown seems to be the determining factor for the lamina/stipe ratio. The relative length of the stipe in the two trees that had been knocked over is much better predicted by the effective height of the crown, rather than by the total length of the trunk.

Although leaf angle was not measured, it was observed that the fronds of the smaller tree ferns are held more erect than those of larger ferns. Functionally, it may be that the more erect leaf angle and the relatively longer stipes on small tree ferns combine to lift the lamina further toward the light. For mechanical reasons, the stipe may have to be shorter to support the more massive, more horizontal lamina of taller tree ferns.

Further investigation is needed to determine what combination of environmental and internal developmental factors determine the relative stipe length and its functional significance. The developmental age of the apical meristem of the fern may be important in determining the lamina/stipe ratio, while the most probable environmental factors would be light intensity and quality.

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An Unusual New Elaphoglossum from Peru

ROLLA TRYON*

A distinctive species of *Elaphoglossum* has been recognized among specimens received for identification from the Missouri Botanical Garden. This new species has a combination of characters that adds to the diversity of its large genus. It also emphasizes the need for more intensive collecting in the species-rich eastern Andes of Peru.

Elaphoglossum pascoense R. Tryon, sp. nov. **Figs. 1, 2.**

Caulis terrestris dorsiventralis valde repens, petioli adaxialiter sulcati fasciculis vascularis sex, phyllopodiis nullis, lamina sterilis oblongo-ovata ca. 12–24 cm longa 6.5–12 cm lata profunde cordata subcuspidata venis liberis longis, lamina fertilis oblonga ca. 12 cm longa 2 cm lata, sporae reticulato-echinatae.

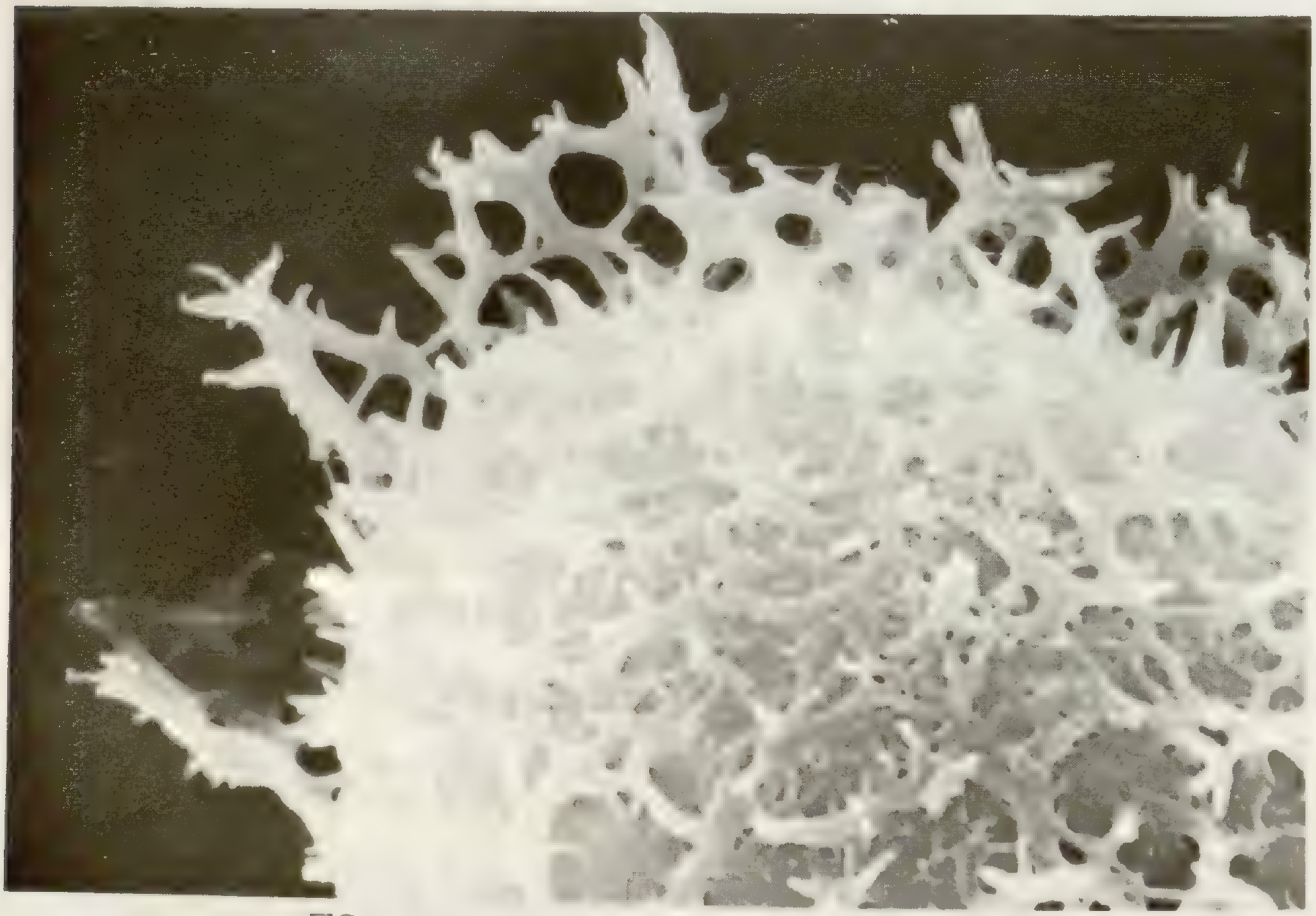

FIG. 1. Spore of *Elaphoglossum pascoense*, ×5555.

Stem with dark, appressed scales, these few except at the apex, stele dorsiventral; leaves 28–54 cm long; petioles gradually merging into (long-decurrent on) the stem, spaced, as long as to usually longer than the lamina, more or less covered by appressed, brown, basally peltate scales; sterile lamina about twice as long as broad, with prominent hydathodes at the vein-ends above, somewhat sparsely covered beneath by elongate, light brown, short-ciliate scales, the costa with appressed brownish scales; fertile lamina densely covered beneath by sporangia, these intermixed with numerous elongate, short-ciliate, brownish scales.

*Harvard University Herbaria, Harvard University, Cambridge, MA 02138.

FIG. 2. Holotype of *Elaphoglossum pascoense*, with fertile leaf in center. ×0.56.

TYPE: Road between Oxapampa and Villa Rica, Dept. Pasco, Peru, 75°20″W, 10°73″S, on flatter parts of steep ridge, 11 October 1982, *Robin B. Foster 9127* (GH; isotypes MO, others to be distributed).

The most unusual features of *Elaphoglossum pascoense* are the relatively broad, deeply cordate sterile lamina with wholly free venation. The sterile lamina can only be compared to that of *E. crinitum,* which has fully areolate venation.

This new species agrees with *Elaphoglossum* sect. *Setosa* (Mickel & Atehortúa, 1980) in the lack of phyllopodia, the long-creeping stem, the presence of hydathodes, and the reticulate-echinate spores. It has the long-creeping stem and dark stem scales of subsect. *Alpestria*. However, it is quite different from all of the enumerated species of that subsection, which have the sterile lamina rather narrow and more or less cuneate at the base.

I am indebted to Dr. Alice F. Tryon for SEM preparations of the spores. This research was partially supported by National Science Foundation Grant DEB 81-05726 to Rolla Tryon and Alice Tryon.

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New Tropical American Ferns

JOHN T. MICKEL*

In the course of identification work for various Latin American field programs at the New York Botanical Garden, several new species of ferns have come to light. Three of the new taxa are in *Anemia*, a genus of which there is yet much to be learned.

10155

Anemia elaphoglossoides Mickel, sp. nov. **Fig. 3B.**

Frondes dimorphae, lamina sterilis indivisa integra glabra coriacea, lamina fertilis bi- ad tripinnata.

Rhizome horizontal, compact, ca. 4 mm diam., clothed with red-orange hairs, 5–8 mm long; fronds clustered, 10–20 cm long, dimorphic, the stipe ½–¾ of the frond length, stramineous, glabrous, slender, 0.5 mm diam., 7–13 cm long; sterile blade simple, elliptic, glabrous, coriaceous, 3.5–4.5 cm long, 1.0–1.2 cm wide, broadly cuneate at the base, the apex obtuse; veins free, dichotomously forking, leaving the midvein at an acute angle; margin thickened; fertile frond about equalling the longest sterile frond in length, bi- to tripinnate; spores unknown.

TYPE: Brazil: Est. Goiás: ca. 15 km S of Niquelândia; gravelly hillside and sandy cerrado, rooted at base of overhanging rock; elev. 1000 m; 21 Jan 1972, *H. S. Irwin et al. 34664* (UB; fragment NY).

Known only from the holotype, two plants, one sterile and one fertile. This is the only known species of *Anemia* with totally undivided sterile blades. Its relationship within the genus probably in subg. *Anemia*, but the precise relationship is not known. The spores are too young to see the ornamentation; the stomates are floating.

10156

Anemia marginata Mickel, sp. nov. **Fig. 2D.**

Frondes dimorphae, lamina sterilis ternata pinnata, segmenta lanceolata coriacea glabra viridi-grisea ad marginem incrassata flava, frondes fertiles bi- ad tripinnatae quam steriles multo longiores.

Rhizome horizontal, compact, short-creeping, ca. 3 mm diam., hairs cream-colored near the apex, maturing to orange-brown; fronds dimorphic; sterile fronds erect, 3.5–7 cm tall; stipe ½–¾ of the frond length, stramineous, glabrous; blade ca. 1 cm broad, ternate; lateral pinnae small, ca. 7 × 3 mm, entire, ovate-lanceolate, ascending, with an acute apex, the base broadly attached; terminal pinna larger, ca. 14 × 4 mm, lanceolate, entire to slightly lobed; blade coriaceous, glabrous; veins free; blade grayish-green with distinct thickened yellow margin, ca. 1 mm broad; fertile fronds erect, 13–15 cm tall, much surpassing the sterile fronds in length, 2–3 pinnate.

TYPE: Brazil: Est. Goiás: Alto Paraiso, Chapada dos Veadeiros, 5 km E of Alto Paraiso, elev. 1600 m; locally common in patches of humus and sand in small level spots near boulders in high sandy flat exposed place; 15 Feb 1979; *Gates & Estabrook 206* (UB; isotype NY).

*New York Botanical Garden, Bronx, NY 10458.

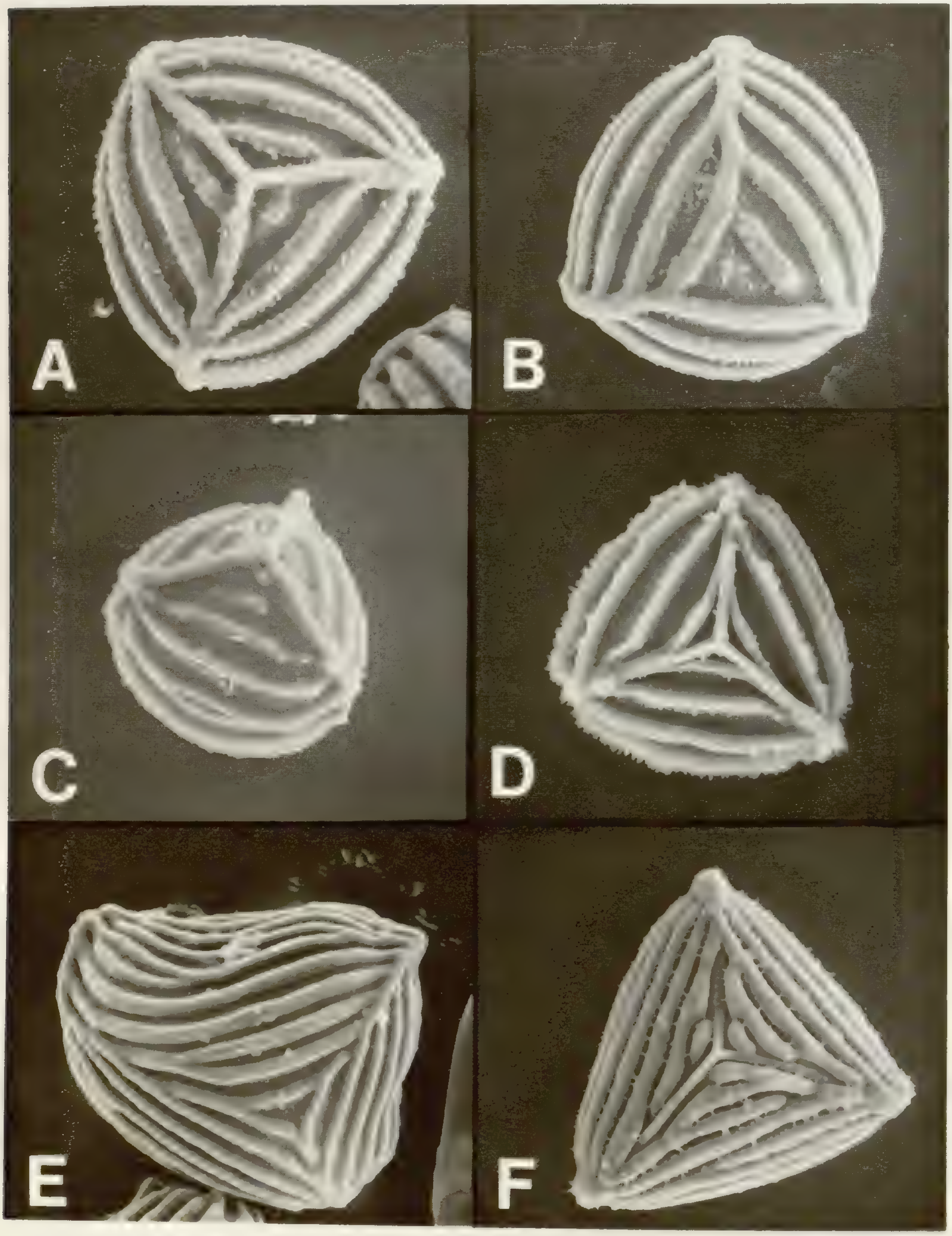

FIG. 1. SEM photomicrographs of *Anemia* spores. A, B. Proximal and distal faces of *A. salvadorensis (Seiler 947)*, ×510. C. Proximal face of *A. sanctae-martae (Steyermark & Rabe 96462)*, ×510. D. Proximal face of *A. hirsuta (Mickel 6241)*, ×510. E. Distal face of *A. oblongifolia (Irwin 34329)*, ×640. F. Proximal face of *A. clinata (Williams 2584)*, ×510.

10157

Anemia salvadorensis Mickel & Seiler,[1] sp. nov. **Fig. 2C.**

Rhizomata adscendentia; frondes usque 17 cm longae, usque 3.5 cm latae; stipes quam lamina sterilis quintuplo brevior; lamina sterilis anguste obovato-oblonga vel oblonga pinnata, sparse pilosa; pinnae steriles 3–9 jugae oblique oblongae obtusae dimidiatae margine denticulatae; nervi liberi; frondium fertilium stipites laminas subaequantes; pinnae fertiles patentes vel oblique adscendentes, a pinnis sterilibus remotae.

Rhizome ascending, clothed with reddish-brown hairs; fronds to 17 cm long, 3.5 cm wide; stipe of sterile frond ca. 1/6 of the frond length, deeply grooved adaxially and laterally, stramineous, wiry, moderately hirsute with reddish, tortuous hairs, glabrate; blade narrowly obovate-oblong or oblong, terminating in a flabelliform or obcordate apical segment, pinnate, thin, dull, sparsely pilose on both surfaces; sterile pinnae 3–9 pairs, subsessile, slightly ascending, to 1.9 cm long, 0.8 cm broad, obliquely oblong, obtuse, strongly inaequilateral at the base (dimidiate), truncate above and cuneate below, erose denticulate, the margin slightly cartilaginous, a distinct midrib lacking; veins free, evident, slightly raised on the adaxial surface; stomates floating; fertile fronds similar to the sterile but longer-stiped, stipes up to half the total frond length, the fertile pinnae 0.7–1.7 cm below the sterile blade; fertile pinnae to 3.2 cm long, spreading to slightly ascending, short-petiolulate, tripinnate, the ultimate divisions slender and virtually lacking lamina; spores tetrahedral-globose, striate, the ridges slender, few, with noticeable space between (6–7 μm, the space being about the same width as the ridges), 76–94 μm diam.

TYPE: El Salvador: Depto. Ahuachapan: Montaña de Agua Prieta, near San Benito, among grass on steep, disturbed, sunny slope, elev. 700 m, 20 Feb 1979, *Seiler 947* (NY; isotypes F, MHNES). Known only from the type collection.

This species is distinct in the habit of the fertile pinnae and pinnate blade. In the habit of the fertile pinnae, the ascending rhizome, and floating stomates it resembles members of subg. *Coptophyllum* sect. *Adetostoma* (*A. brandegeea*, *A. intermedia*, and *A. clinata*), which are found in western Mexico (the first two) and Panama to Bolivia (*A. clinata*), according to Mickel (1962, 1966). However, the pinna form is more like that of *A. sanctae-martae* of Colombia, and in form of the pinnae except for their undivided nature like that of the more ubiquitous *A. hirsuta*, which is closely related to *A. sanctae-martae* (subg. *Anemia* sect. *Hirsutae)*. The very narrow form of the blade and the very short stipe suggest a relationship to *A. oblongifolia* (subg. *Anemia* sect. *Oblongifoliae*). The spores of *A. salvadorensis* most closely resemble those of the *A. hirsuta* complex (incl. *A. sanctae-martae*) (*Figs. 1A–E*). Thus, although the precise relationships are not clear, it is our conclusion that the new species represents a pivotal position in the evolution of the genus, lying somewhere between the three sections mentioned above.

The section *Adetostoma* was placed in subg. *Coptophyllum* largely on the basis of its spores with many closely set ridges, as in *A. clinata (Fig. 1F)* (Mickel, 1962). The floating stomates were thought to be an anomaly or advanced feature in that subgenus. On the other hand, they are known in some species of subg. *Anemiorrhiza* and in all species of subg. *Anemia*. On the basis of the ascending rhizome, the

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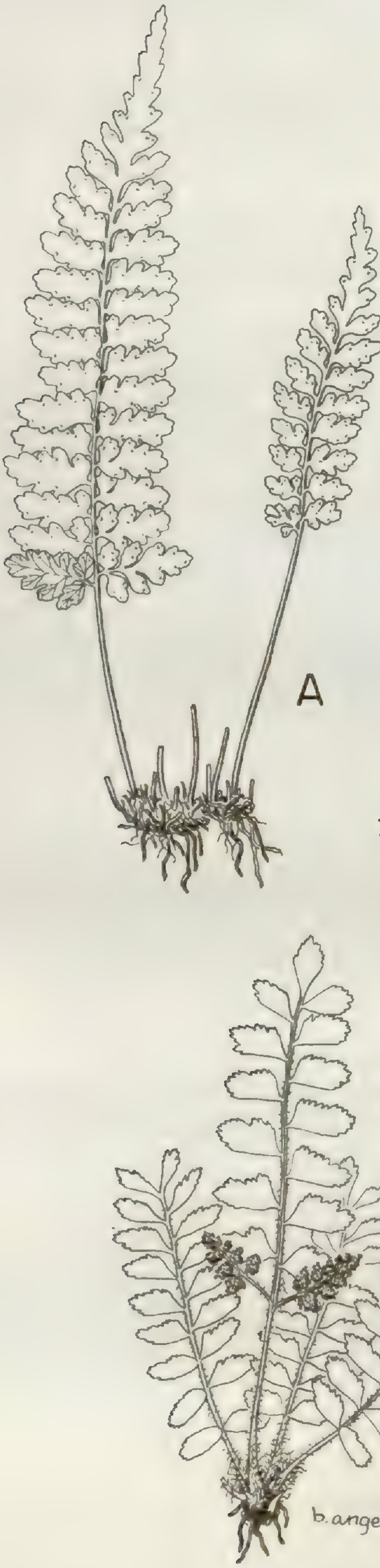
[1]Mr. Seiler served for two years in the Peace Corps in El Salvador. During this time he traveled through much of the country collecting plants and preparing specimens for the herbarium of the Museo de Historia Natural de El Salvador (MHNES).



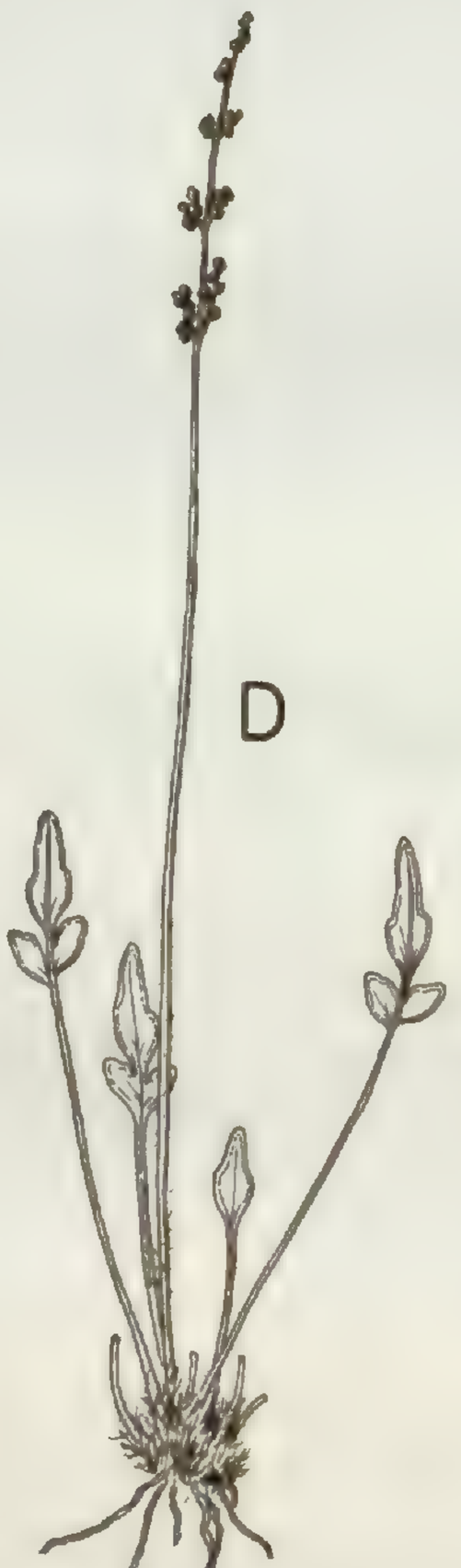


FIG. 2. A. Habit of *Saccoloma membranaceum*. B. Pinna of *S. membranaceum*. C. Habit of *Anemia salvadorensis*. D. Habit of *Anemia marginata*.

floating stomates, and the distinctive, obliquely held fertile pinnae, we would place the new species in sect. *Adetostoma,* but with the similarities to sect. *Hirsutae* and sect. *Oblongifoliae* of subg. *Anemia,* we would also remove sect. *Adetostoma* from subg. *Coptophyllum* and place it in subg. *Anemia*.

Patent fertile pinnae are known from several groups within the genus *Anemia: A. aspera* and *A. perrieriana* (subg. *Coptophyllum* sect. *Anemiaebotrys*), *A. elegans* and *A. eximia* (subg. *Coptophyllum* sect. *Trochopteris*), *A. colimensis* (subg. *Anemiorrhiza*) and all of sect. *Adetostoma* (subg. *Anemia*). These four groups are probably not closely related, and whether any of them actually represents the ancestral type in the genus is not known. It is clear that the patent fertile pinnae represent the primitive condition in the genus (Mickel, 1967), being derived from fronds with sporangia distributed over the abaxial surface and then limited to the basal pair of pinnae, but it is not known whether the four groups within the genus today that have patent fertile pinnae are remnants of this condition or whether they are reversions to this condition. There are very likely other species of *Anemia* to be found in Latin America that hopefully will shed light on the phylogenetic relationships within the genus.

10157

Asplenium acutiserratum (Hieron.) Mickel, comb. nov.

10158 *Asplenium cirrhatum* L. C. Rich. var. *acutiserratum* Hieron., Hedwigia 60:259. 1919, as "*acutiserrata.*" LECTOTYPE (selected here): Trinidad, *Fendler 140* (presumably B; isolectotype NY).

1877

Asplenium longicaudatum Mickel & Stolze, sp. nov. **Fig. 3A.**

Ab. *A. cirrhato* Rich. ex Willd. frondibus grandibus et apice pinnarum acuto differt.

Plants terrestrial; rhizome stout, erect, provided with lanceolate to ovate, acute scales, these 2–4 mm long, 0.6–1.0 mm wide, dark brown or (more commonly) bicolorous, with narrow, lighter brown margins, subclathrate, the lumina isodiametric or slightly longer than broad; fronds 70–100 cm long, 12–18 cm broad, pinnate; petiole 10–30 cm long, terete, dark brown to atropurpureous, lustrous or sublustrous, nonalate, glabrous, or with a few broad scales at base; blade lanceolate or deltoid-lanceolate, not or scarcely reduced at base, abruptly and strongly tapering to a radicant apex; lamina thin-herbaceous, yellowish-green to gray-green, essentially glabrous; rachis dark reddish-brown, lustrous, terminating in a long, flagelliform apex, with the tip proliferous; pinnae 8–14, subdistant, to 10 cm long and 1.5 cm wide, sessile or short-petiolulate, equilateral except at the base, there broadly cuneate to truncate acroscopically, narrowly cuneate basiscopically, attenuate at the apex, margins subentire to broadly crenulate; veins indistinct or obscure, commonly once-forked; sori 5–8 mm long, linear to narrowly oblong, slightly arcuate; indusium linear, yellowish, firm-textured, subentire.

TYPE: Ecuador: Pcia. Morona-Santiago: Cordillera Cutucú, ridge between Ríos Itzintza and Chupiasa, 1200–1350 m, *Camp E-1283* (NY; isotype S).

This species belongs to the *A. radicans* complex. It is somewhat similar to the widespread *A. cirrhatum* in that they are both once pinnate, but the latter is considerably smaller with obtuse to subacute pinna apices. It resembles even more closely *A. acutiserratum* (Hieron.) Mickel of Trinidad, which has acuminate pinna apices but with serrate pinna margins, auriculate pinna bases, and the fronds normally reach 35–45 cm in length.

FIG. 3. A. Habit of *Asplenium longicaudatum*. B. Habit of *Anemia elaphoglossoides*. C. Habit of *Grammitis kirkbridei*.

Grammitis kirkbridei Mickel, sp. nov. **Fig. 3C.**

Ab *G. knightii* (Copel.) Seymour frondibus parvioribus, lobis approximatioribus, stipitibus brevioribus differt. Haec species Joseph H. Kirkbride, Jr. botanico dicatur.

Plants epiphytic; rhizome erect, ca. 0.6 mm diam, clothed with yellow-brown, lanceolate scales ca. 1 mm long; fronds fasciculate, 3–5 cm long, 5–9 mm wide; stipes 3–9 mm long, clothed with stiff, spreading, reddish-brown hairs 1–1.5 mm long; blade pinnatifid, cut ½–⅔ to the midvein, the lobes obtuse, slightly ascending, 10–13 pairs, with abundant, stiff, erect, reddish-brown hairs ca. 0.4 mm long; veins obscure; sori mostly 3 or 4 pairs per lobe, ca. 1 mm diam., medial between the midvein and the margin, which is often slightly recurved.

TYPE: Panama: Pcia. Darién: Tres Bocas on the Río Coasi, 1 May 1968, *J. H. Kirkbride Jr. & J. A. Duke 1381* (NY).

Grammitis kirkbridei belongs to the group of *G. basiattenuata* (Jenm.) Proctor of the West Indies and *G. truncicola* (Klotzsch) Morton of South America, but has fewer lobes and shorter laminar hairs. It most nearly resembles *G. knightii* (Copel.) Seymour, from which it differs in its smaller, less deeply cut fronds, pinnae closer together, and shorter stipe.

Polystichum hottense C. Chr. **Figs. 4A, B.**

For many years this species was known only from the type collection from the Massif de la Hotte in southwesternmost Haiti *(Ekman H-10130)* and part of a mixed collection from Ma Blanche, Haiti *(Ekman H-513)*. It has recently been collected at the mining site of Las Abejas, Prov. Pedernales, in southwestern Dominican Republic *(Liogier 14173, 26784; Mickel 8168; Zanoni 16718)*. This striking plant with bipinnate fronds and abundant, spreading, often black-centered rachis scales has never been well illustrated and is thus presented here.

10162

Pteris striphnophylla Mickel, sp. nov. **Figs. 4C, D.**

Ab *P. longifolia* L. frondibus parvis, lamina sclerotica glabra, apice pinnarum obtuso differt.

Plants terrestrial; rhizome horizontal, compact, the scales linear, stramineous to light brown, 1.5–2.5 mm long, in a tangle of wiry roots and old stipe bases; stipes 2–4 cm long with hairs grading to narrow scales at the base; fronds approximate, 7–11 cm long, 1.5–2.4 cm wide, pinnate, with a conform terminal pinna; pinnae 6–9 pairs, mostly 10–12 mm long and 4–5 mm wide, entire, elliptic, the apex obtuse, the base rounded to cordate, extremely coriaceous, pinna attachment to the rachis swollen, the pinnae tending to be deciduous; veins obscure, free, simple or 1-forked; blade glabrous except for a few short hairs at pinna attachment; sori continuous along the margin, interrupted only at the pinna apex; indusium strongly coriaceous.

TYPE: Dominican Republic: Pcia. Pedernales: Sierra de Baoruco, El Pon, from Las Mercedes to Aceitillar, 1000 m, growing in a ravine, in the cracks of limestone rock cliff, 11 Feb 1969, *Bro. Alain Liogier 13798* (NY; isotype JBSD).

This is clearly related to *P. longifolia*, judging from its dissection, rhizome scales, spores, cordate pinna bases, swollen pinna attachments, and lack of axis awns. It is easily distinguished by its small size, glabrous blade, and heavily coriaceous texture.

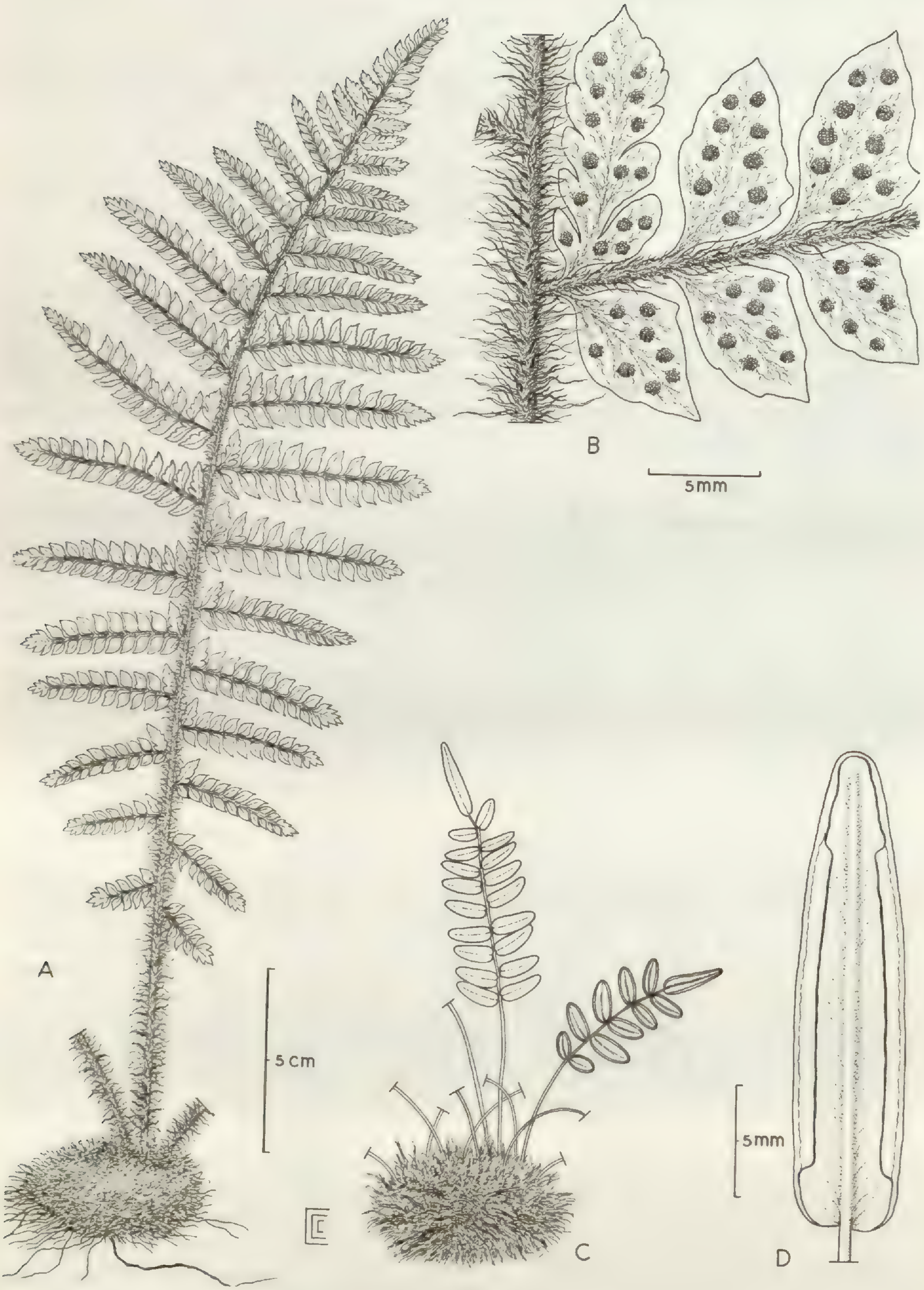


FIG. 4. A. Habit of *Polystichum hottense (Liogier 14173)*. B. Same, rachis and pinna base. C. Habit of *Pteris striphnophylla*. D. Same, pinna.

Saccoloma membranaceum Mickel, sp. nov. **Figs. 2A, B.**

Ab aliis speciebus generis frondibus parvibus et lamina membranacea differt.

Rhizome horizontal, short-creeping, 2–3 mm diam., with coarse, black, wiry roots 0.4–0.6 mm diam.; rhizome clothed with lustrous, reddish-brown, heavily indurated, linear-deltate scales 1–3 mm long; fronds many, approximate, 10–14 cm long, 2.0–3.4 mm wide; stipe 2–3 cm long, castaneous to light brown, glabrous, 0.3–0.4 mm diam.; blade narrowly lanceolate, 1-pinnate to a pinnatifid apex, the pinnae shallowly to deeply lobed, the basal pinnae often with a pair of free lobes, the upper pinnae cut less than ½ way to the midvein, the basal acroscopic lobe slightly exaggerated; veins free, mostly simple or dichotomously forking, more divided in larger lobes; lamina membranous, glabrous; sori terminal on veins, ca. 1 mm from the margin, indusia cup-shaped; spores tetrahedral, with low, dichotomously branching ridges.

TYPE: Brazil: Est. Acre: Cruzeiro do Sul, Rio Jurua and Rio Moa, Serra do Moa, Rio Moa 6 km above school; forest on mountain; 25 Apr 1971, *Prance et al. 12432* (INPA; isotype NY).

The label states that the type specimen is epiphytic, but the roots hold considerable sand and all the relatives are strictly terrestrial.

This species is strikingly different from other members of the genus in size and texture. The spores are similar to those illustrated by Tryon and Tryon (1982, p. 386) in their low, dichotomously forking ridges. The rhizome scales and sorus structure and location also support its placement in *Saccoloma*.

ACKNOWLEDGMENTS

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SHORTER NOTE

An Urban Locality For Asplenium platyneuron—The ebony spleenwort, *Asplenium platyneuron* (L.) B.S.P., was recently discovered at a site in Brooklyn (Kings County), New York. Vouchers consisting of only sterile fronds are deposited at BKL (*W. Sax-Cedar & J. Goldbaum,* 15 Feb 1984; *T.J. Delendick,* 22 Feb 1984). The population consists of fourteen individuals growing in a vertical stone wall at a well-developed and heavily trafficked intersection in the Park Slope district, approximately midway between Prospect Park and the Gowanus Canal. The wall is part of an access well to a below-ground basement entrance to a commercial building. The well is approximately 12 feet deep, 5 feet wide and 40 feet long, with an east-west orientation. The ferns occur in the uppermost seven feet of the wall, among clumps of moss in the mortar between the granite stones; they are restricted to the east end of the well, thus having a western exposure. None of the plants examined had fertile fronds.

This Brooklyn station represents the second verified locality for *A. platyneuron* known to exist on western Long Island at the present time, and the only one which is current for Kings County. The other site for the species in the western portion of the island is at Fort Totten on the north shore of Queens County, reported by Greller and Locke (Amer. Fern J. 73:6–8. 1983). This situation contrasts strongly with the distribution of the species on Long Island in the 19th and early 20th Century, when it was noted as "frequent throughout the island" by Jelliffe (The Flora of Long Island, 1899), including at least three locales in Kings County: East New York, *G. B. Brainerd* in 1866; Rockaway Beach, *G.D. Hulst* in 1889; and Central Park [now designated as Prospect Park], *J. McCallum* in 1902 (all BKL). It is, or at any rate was, fairly common in the eastern counties of Nassau and Suffolk. Stalter, (Bull. So. Carolina Acad. Sci. 41:72. 1979) cited it as occurring on Long Island, and the late Stanley Smith of the New York State Museum, Albany, noted it in both Nassau and Suffolk counties (manuscript checklist).

This find also represents the only current site for *A. platyneuron* on Long Island south of the terminal moraine that forms the backbone of the island. There is a specimen of the species at BKL from Rockaway Beach (Kings County, 1889) and at NY from Valley Stream, Nassau County (*Bicknell,* 8 Aug 1903). The latter includes the collector's note, "Bank of Aqueduct causeway. The only plants I have found south of the terminal moraine." The outwash plains from the glacial moraine which form the southern portion of Long Island provide few habitats suitable for *Asplenium* species. The occurrence of *A. platyneuron* there seems, on the basis of available data, to be restricted entirely to man-made sites. It is remarkable that *A. platyneuron* has been able to extend its range into an area which has been so long and so heavily used as to lack virtually any trace of the original flora, and that its extension was made possible through commercial development.

I am grateful for the assistance of Wynne Sax-Cedar, who made the first collections from the newly discovered locale, and to Andrew Greller and Richard Stalter for their comments and review of the text.—*Thomas J. Delendick, Brooklyn Botanic Garden, 1000 Washington Ave., Brooklyn, NY 11225.*

AMERICAN FERN JOURNAL

Manuscripts submitted to the JOURNAL are reviewed for scientific content by one or more of the editors and, often, by one or more outside reviewers as well. During the past year we have received the kind assistance of J .D. Caponetti, W. D. Hitz, H. T. Horner, Jr., J. D. Montgomery, M. G. Price, H. E. Robinson, A. R. Smith, R. G. Stolze, W. C. Taylor, D. P. Whittier, E. Wollenweber, and J. J. Wurdack, to whom we are deeply indebted. We welcome suggestions of other reviewers.

Dr. Alan R. Smith, Department of Botany, University of California, Berkeley, CA 94720, will become editor of the American Fern Journal effective 1 Jan 1985. Dr. David B. Lellinger, U. S. Nat'l. Herbarium NHB-166, Smithsonian Institution, Washington, DC 20560, will become editor of Pteridologia on the same date.

—D.B.L.

1985 A.I.B.S. MEETING–CALL FOR PAPERS

The American Fern Society and the Botanical Society of America will meet with the A.I.B.S. Annual Meeting at the University of Florida, Gainesville, on 11—15 August 1985. Those members of the American Fern Society wishing to present a paper or poster and who have not received abstract forms may obtain forms from the program chairman of the Pteridological Section of the Botanical Society: Dr. Christopher Haufler, Dept. of Botany, University of Kansas, Lawrence, KS 66045.

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Page 59, line 27: For "recreense" read "recreensis."
Page 60, lines 23 and 24: For "Gaulterio" read "Gualterio."

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